POSTBREEDING ECOLOGY OF SHOREBIRDS ON THE

ARCTIC COASTAL PLAIN OF ALASKA

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ABSTRACT

Previous research on the Arctic Coastal Plain (ACP) of Alaska has shown that postbreeding shorebirds congregate at coastal sites prior to fall migration. Relatively little has been done to compare distribution, community characteristics, or behavior broadly across the ACP landscape, but this information is necessary to set the context for interpreting population demographics and setting conservation priorities.

I collected data on distribution, species composition, phenology, and habitat use of postbreeding shorebirds in 2005-2007. I found that distribution of shorebirds across the ACP was not uniform: I identified persistent "hotspots" at Peard Bay, Pt. Barrow/Elson Lagoon, Cape Simpson, Smith Bay to Cape Halkett, and at the Sagavanirktok and Kongakut Deltas. Staging phenology varied by species and location, and differed than that reported in previous studies for several species. Three foraging habitat guilds existed with birds favoring gravel beach, mudflat, or salt marsh/pond edge habitats.

Using VHF telemetry, I examined how shorebirds moved from tundra breeding sites to and between coastal postbreeding sites. I found that most species exhibited a variable direction of movement compared to their ultimate migration direction; this may be related to each species' overall length of stay on the ACP. I also found species-specific patterns of movements and residence time that were indicative of differing life history strategies.

Lastly, I examined the use of physiological tools (triglyceride and corticosterone levels) to assess function and quality of foraging sites for postbreeding shorebirds, taking into account varying molt strategies. I determined that molt strategies affected physiological profiles and physiologic metrics varied through space and time. However, my hypotheses for variation in physiological patterns for shorebirds employing different molt strategies and using sites of varying quality were not completely upheld. I suggest that assessments of site quality for postbreeding shorebirds should consider species-specific life history strategies, and use multiple species and physiological metrics as indicators.

Given suspected declines in North American shorebird populations, and accelerated rates of environmental change in northern Alaska, this contextual information regarding postbreeding distribution, population characteristics, behavior, and physiology may help interpret changes in shorebird populations or behavior and establish strategies to protect important habitat.

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PREFACE

This dissertation was written as three data chapters, all formatted as manuscripts for peer-reviewed journals. The first chapter is formatted for (and published in) *Arctic*, the second chapter is formatted for (and submitted to) *Condor*, and the third chapter is formatted for submission to *Auk*. While the dissertation is single-authored, each manuscript is co-authored by a number of excellent scientists with whom I was privileged to work while doing this research. Therefore, the "we" in each chapter refers to the group of authors listed, but I alone am responsible for any errors.

Conducting research in remote Arctic Alaska is somewhat costly, and I received funding for this project from many sources. The Minerals Management Service (now the Bureau of Ocean Energy Management, Regulation, and Enforcement) provided the lion's share of funding through competitive research grants from the Coastal Marine Institute. Additional funds for research and logistics were provided by the U.S. Fish Wildlife Service (Division of Migratory Bird Management and Arctic National Wildlife Refuge), the U.S. Geological Survey (Quick Response Program), the Bureau of Land Management (Fairbanks District Office), ConocoPhillips Alaska, Inc., BP Exploration (Alaska) Inc., Manomet Center for Conservation Sciences, Sigma Xi, and the Arctic Audubon Society. I am grateful for all of these entities' support of my research.

This project would not have been possible without the dedication and hard work of a huge number of people. I would like to extend much gratitude to my academic

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Many fellow graduate students have provided encouragement, insight, and commiseration through the years. Although too numerous to name them all, I would particularly like to thank Julie Morse, Rebecca Bentzen, Chrissy Apodaca, Trish Miller, Stacia Backensto, River Gates, Mike Knoche, and Roy Churchwell, and I apologize to anyone whose name I did not mention. Similarly (as in being too numerous to name), I am grateful to the many paid and volunteer field technicians who spent countless hours counting, catching, bleeding, and listening for shorebirds in unpleasant weather and under

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1. INTRODUCTION

> The restlessness of shorebirds, their kinship with the distance and swift seasons, the wistful signal of their voices down the long coastlines of the world make them, for me, the most affecting of wild creatures.
>
> - Peter Matthiessen, *The Wind Birds*, 1973

The ultimate goal of this dissertation was to examine landscape-scale patterns in post-breeding shorebird distribution, phenology, species composition, habitat use, and large-scale movements, and relate these to how Alaska's Arctic Coastal Plain (ACP) functions for shorebirds prior to fall migration given species-specific life history strategies. This information may fill gaps in the contextual framework needed to accurately estimate and interpret demographic parameters, such as postbreeding population sizes or post-fledging survival, which assist with understanding population trends and setting conservation priorities. It also represents a first attempt to link large-scale patterns of postbreeding shorebird use with underlying ecological processes (pre-migratory shorebird physiology) in Arctic Alaska; this linkage is a tenet of the landscape ecology approach to conservation and management (Turner 1989, Wu and Hobbs 2007). An associated conservation-related goal was to evaluate different methods for assessing

relative site importance for postbreeding shorebirds, given species-specific differences in biology that will be gleaned from this research.

Much of the work done by wildlife scientists involves enumerating populations of animals and determining vital rates such as productivity and survival in different habitats. While this may seem relatively straightforward in theory, in practice estimation and interpretation of population demographics requires a substantial body of supporting knowledge about the population in question and its habitat. The distribution of animals across a landscape (uniform or patchy?), habitat use (selective at what scale?), movement patterns (within or out of the study area?), behavior at sites within the larger landscape (all similar or some unique?), response to environmental cues and changes, and/or important associations with other organisms are some of the questions that should be answered to place demographic information into the appropriate context, and enable the application of this information to solving management and conservation problems. Keppie (2006) defined context as "the setting or circumstances in which an event or behavior of interest occurs," and heralded it as a critically important concept in ecological research and resource management because it affects our interpretation of the world around us.

It is helpful to organize the collection of contextual information for a particular species or system around a unifying theme that may enable us to hypothesize and then explain the patterns observed. This approach places the study of natural history patterns and processes into the realm of deductive (as opposed to inductive) reasoning. For birds,

life history strategies organize the sequence and timing of life history events throughout the annual cycle of individuals and populations, and can dictate the function of a particular habitat or landscape for birds at different stages or times of the year. Accordingly, comparing differences in life history strategies among species and hypothesizing how these differences may result in species-specific variation in ecological patterns provides a useful framework for collecting and interpreting contextual information needed for understanding population characteristics on a large scale.

Reproduction, molt, and migration are probably the three most important events in the life cycle of migratory birds (Thompson and Leu 1994). Scheduling these events forms the basis for evolution of many avian life history strategies, because selection favors the non-overlap of these energetically intensive events (Payne 1972, O'Hara et al. 2002). After the short reproductive season, Arctic-breeding shorebirds spend the remainder of their annual cycle balancing the demands of migration and molt. These species exhibit a variety of life history strategies with respect to overall migration distance (Holmes 1966a), length of individual migratory flights (Piersma 1987), and timing of prebasic molt relative to fall migration (Noskov et al. 1999, Barta et al. 2008). How variation in these strategies influences migratory shorebirds' ecology has been well studied in some species and systems, but not in others. Substantial contextual information exists regarding spring migration for Arctic-breeding shorebirds (including the transition from wintering to migratory state; e.g., Butler and Kaiser 1995, Lyons and Haig 1995, Iverson et al. 1996, Warnock and Bishop 1998, Williams et al. 2007), but

fewer studies have been published on fall migration ecology (but see for example Butler et al. 1987, O'Reilly and Wingfield 1995, Acevedo Seaman et al. 2006), and fewer still on the ecology of the postbreeding/pre-migratory period that occurs while many shorebirds are still in the Arctic preparing for southbound migration. This period in the annual cycle of shorebirds has often been studied ancillary to or as part of breeding or migration ecology research because it spans the transitional period between these two major events in a bird's annual cycle. However, the postbreeding period may involve distinct patterns of behavior, physiology, and habitat use that are dependent on each species' life history strategy.

To date, only a few researchers have investigated postbreeding ecology of shorebirds on the Arctic Coastal Plain (ACP) of northern Alaska (Fig. 1.1; Table 1.1). Frank Pitelka and his students Dick Holmes and Peter Connors contributed much to our understanding of various aspects of breeding and postbreeding ecology of one or more species in Barrow, Alaska. In particular, Holmes (1966a, 1966b, 1971, 1972) elucidated patterns in breeding ecology and molt timing in Dunlin (*Calidris alpina*) and Western Sandpipers (*C. mauri*) that highlighted how each species differed in scheduling of life history events in response to their extreme environment. He related these differences to species' overall length of migration and the peak of invertebrate prey availability in the Arctic. In contrast to most other shorebird species breeding in northern Alaska, Dunlin, which are shorter-distance migrants, initiate flight and body feather molt at breeding sites and complete the majority of molt activity during the postbreeding period. Holmes

(1966a) hypothesized that this strategy enabled Dunlin to exploit the limited food resources available in the Arctic during late summer for completing molt and pre-migratory fuel deposition. In contrast, longer-distance migrants (e.g. Western Sandpipers), for which selection favored early departure from breeding areas, did not utilize Arctic food resources for molt or pre-migratory fueling (Holmes 1966b, 1972). Connors (1983, 1984) and Connors et al. (1979, 1981) examined postbreeding habitat use, diets, annual and geographic variation in densities, and qualitative pre-migratory fat deposition trends for a suite of shorebirds using coastal areas at Barrow and several other sites. These intensive studies documented a marked shift of shorebirds from tundra breeding habitat to coastal (littoral) habitat during the postbreeding period. Densities of each common species varied between gravel beach, mud flat, and slough edge habitat, which caused distribution of individuals and species among sites to be non-uniform. Among other noteworthy findings, Connors (1984) determined that pre-migratory fat deposition in relation to the speed and timing of migration (based on mean fat scores changing through time) differed across species: Red Phalaropes (*Phalaropus fulicaria*) and Dunlin showed a significant increase in fat scores with date and remained late into the season at postbreeding sites, whereas Semipalmated Sandpipers (*C. pusilla*) left the Arctic sooner and with only moderate fat scores. Although these authors did not explicitly ask "how does life history strategy affect postbreeding ecology and/or physiology?" their data are useful for addressing this issue.

Other studies have also contributed to our understanding of the context of shorebird postbreeding ecology, mainly in terms of what sites/habitats are frequented by which species after the breeding season. Many of these studies have focused on a single site that was thought to be important to one or more bird species (not always shorebirds in particular). Although the results of these site-specific studies are at times contradictory, they provide a comparative perspective of shorebird use of the ACP littoral zone across years and taxa. For example, postbreeding shorebirds at Icy Cape, Alaska (located on the Chukchi Sea coast in Kasegaluk Lagoon; Fig. 1.1) used both gravel beach and salt marsh habitat (Lehnhausen and Quinlan 1981), whereas Connors and Risebrough (1977) found that gravel beach was used by postbreeding shorebirds in the Beaufort Sea while salt marsh was used primarily in the Chukchi Sea. Aerial surveys for marine birds conducted across the entirety of Kasegaluk Lagoon (surrounding Icy Cape, Fig. 1.1) documented that shorebird densities were variable across years, the peak of abundance of small shorebirds was in late August, and shorebirds were mostly observed in mudflat habitat (Johnson et al. 1993). Habitat use, abundance, and timing of shorebird use of Peard Bay (also on the Chukchi Sea coast, Fig. 1.1) were similar to that at nearby Icy Cape (Gill et al. 1985). Dunlin and Sanderlings appeared to prefer mudflat habitat at the Colville River Delta (on the Beaufort Sea coast; Fig. 1.1) while all other species were equally distributed between mudflat and salt marsh habitat (Andres 1989). Martin and Moiteret (1981) suggested that wind and weather events on the Canning River Delta (located between the Sagavanirktok and Okpilak Deltas on the Beaufort Sea coast; Fig.

1.1) created variability in food resources that affected the distribution and abundance of foraging shorebirds. Aerial surveys conducted across the Arctic National Wildlife Refuge found that phalaropes used open-water areas close to barrier islands more than areas in the middle of coastal lagoons; this may also have been related to spatial variability of food resources (Spindler 1979).

Most of these studies were focused on reporting trends in the timing and spatial context of shorebird use of each site, and few tied their observations to life history strategies of individual species or the comparative function of the overall landscape for postbreeding shorebirds. An overarching theme of many of the above-referenced studies is that postbreeding ecology of shorebirds on the ACP is characterized by high spatial and temporal variation. Studies conducted over one or two years at one or a few sites are likely to capture elements of that variation rather than underlying patterns of shorebird behavior, habitat use, or migration phenology. Without planned simultaneous replication of both spatial and temporal variation, it is difficult to scale up contextual information, e.g. to assess the importance of certain sites/habitats through time or investigate commonalities of behavior or phenology. Alternative models of studying broad ecological patterns exist, as with the top-down "macroecology" approach to examining the partitioning of food and space resources among individuals and species (Brown and Maurer 1989, Brown 1995). For example, studies of marine bird distribution often focus on identifying "hotspots" or concentration areas across a continuous and dynamic landscape rather than on studying use at a given site, because conditions in the marine or

nearshore environment vary widely in space and time (Suryan et al. 2006, Yen et al. 2006). Individual sites themselves may not be as critically important as the spatial arrangement of adequate foraging habitat across an unpredictable environment like northern Alaska (e.g., Skagen and Knopf 1993, Skagen and Knopf 1994, Haig et al. 1998). However, no study to date has attempted to examine shorebird distribution and movements across the littoral zone of the ACP landscape to assess the presence of hotspots or spatial connectivity between sites.

The overall goals of this dissertation are accomplished in a series of steps that move from the more descriptive (Chapters 2 and 3) to the more theoretical (Chapter 4), although I attempted to maintain relevance to critical management and conservation issues throughout. In Chapter 2, I used a landscape-scale approach to address the issue of high spatial variability in comparing and contrasting postbreeding shorebird ecology across a region as large as the ACP. This was done in hopes of resolving the problem of having to induce large-scale commonalities from site-specific research. First, I conducted aerial surveys across the entire length of the ACP littoral zone in a series of repeat surveys over two years to locate hotspots of postbreeding shorebird abundance. The advantage of this approach was that it enabled me to compare the relative abundance of birds at a scale that addressed regional distribution patterns. I also examined community composition and diversity patterns, phenology, and habitat use at six individual sites across the ACP. I compared patterns in postbreeding ecology across sites that were representative of different landforms on the ACP (e.g. large river deltas and

barrier island/lagoon complexes) but that also spanned the geographic range of the study area. Additionally, I compared my data, collected following thirty years of potential climate and environmental change, to published data from the studies highlighted above.

In Chapter 3 I used VHF radio telemetry on five common species (Dunlin, Semipalmated Sandpipers, Western Sandpipers, Red Phalaropes, and Red-necked Phalaropes [*Phalaropus lobatus*]) to examine residence time at and movements of individuals among sites across the ACP. I assumed that variation in residence time and movements of postbreeding shorebirds was a function of life history characteristics; specifically, differences in migration routes and in timing of prebasic molt that may occur between species or even individuals within a species (e.g., Warnock and Bishop 1998). I tested two predictions: (1) that shorebirds' direction of movement during the postbreeding period would be reflective of their ultimate migration direction, and (2) that the timing of prebasic molt in relation to fall migration would be more important than overall migration distance for influencing residence time and movements. This part of my research also had implications for how interconnected postbreeding sites on the ACP were, and how monitoring methods like broad-based aerial surveys should be designed to incorporate knowledge regarding spatial connectivity and the propensity of shorebirds to move rapidly between sites.

Chapter 4 focuses on the physiological mechanisms underpinning shorebird behavior, and provides a more individualistic approach to understanding postbreeding distributions. While aerial or ground surveys for density or abundance provide an

assessment of site importance, they may fail to take into account how life history strategies affect behavior and physiology and therefore the function of a given site for each of the species present. In this chapter I used plasma metabolite and hormone analyses to evaluate physiological profiles for captured individuals of three species: Dunlin, Semipalmated Sandpipers, and Western Sandpipers. I predicted that physiological metrics indicating fueling rates (triglyceride levels) and migratory "preparedness" (baseline corticosterone levels) would be reflective of each species' molt and migration strategies, but within those constraints, could indicate how well a site was contributing to individuals' ability to prepare for southbound migration. Thus, a comparative assessment of population-level physiologic indicators at each postbreeding site could inform an evaluation of both site function (across species) and site quality (within a species). This information should be valuable to managers wishing to understand comparative site relevance across a large landscape for multiple species of shorebirds.

From a management and conservation perspective, this research is timely. Arctic-breeding shorebirds in North America are thought to be decreasing in abundance (Bart et al. 2007), and worldwide, 54% of shorebird species that are largely confined to breeding in the Arctic are reported to be in decline (Sitters and Tomkovich 2010). The reasons for these declines are myriad and likely include: habitat loss from wetland modification, agriculture intensification, and decreasing Arctic tundra extent; declining food resources and reduced habitat suitability at staging/stopover sites due to human activity;

disturbance from fishing and aquaculture farming at important wintering and migration areas, and from oil and gas exploration in the Arctic; and a changing coastal environment worldwide (International Wader Study Group 2003, Sitters and Tomkovich 2010). Many of these factors affecting shorebird declines are likely to increase in severity in the future: for example, up to 51% of tundra habitat worldwide is expected to be lost by 2100 due to northward encroachment of treeline (Callaghan et al. 2005), and wetland modification in areas outside North America (such as the Saemangeum Estuary in South Korea) is ongoing (Moores et al. 2006). On the other hand, overharvesting of shorebird food resources (such as horseshoe crab eggs in Delaware Bay and shellfish in the Dutch Wadden Sea) has been recognized as harmful to shorebird populations and steps have been taken to regulate these activities (Sitters and Tomkovich 2010). It is difficult to predict with certainty the overall influence of these factors on shorebird populations, not only because their long-term trajectories are uncertain, but also because comparatively little is known about the magnitude of shorebird declines for many species and whether they represent natural population fluctuations or long-term, downward trends (Gratto-Trevor et al. 2001, Morrison et al. 2001). Deciphering this mystery will require long-term analysis of trends in population size and demographics (and the appropriate contextual information needed for interpretation of these), and enhanced knowledge regarding the sensitivity of life history characteristics to environmental or anthropogenic change.

Particularly cogent to shorebird populations in Arctic Alaska is that fact that oil and gas exploration and development is a potential use of almost all of the National Petroleum Reserve –Alaska (NPR-A), and of coastal and nearshore areas of the Chukchi and Beaufort Seas. Opening of the coastal 1002 Area of the Arctic National Wildlife Refuge to oil and gas interests has been proposed and will likely resurface politically in years to come. Exploration and development activities could decrease suitable habitat for postbreeding shorebirds because shorebirds are concentrated in high densities at coastal areas during this period of time, making them susceptible to impacts from oil spills or infrastructure development (Taylor et al. 2010). Information on species-specific ecology during the little-studied postbreeding period, such as will be provided in this dissertation, will help inform environmental impact evaluations and assist in developing mitigation plans for future oil and gas impacts, and can be fed into the adaptive management framework being utilized by resource agencies to facilitate effective and sustainable decision making (Lee 1999). Adaptive management views management actions as "experiments" in which outcomes inform later policy choices. However, experiments at scales like that of the ACP risk unanticipated outcomes that are beyond the control of managers to reverse (Chapin et al. 2010). Therefore, information on status and trends in avian biodiversity at scales encompassing the entire ACP will be critical to designing and informing management actions that are appropriate for application across an environmentally changing and politically volatile landscape.

Literature cited

Acevedo Seaman, D.A., C.G. Guglielmo, R.W. Elner, and T.D. Williams. 2006. Landscape-scale physiology: site differences in refueling rates indicated by plasma metabolite analysis in free-living migratory sandpipers. Auk 123:563-574.

Andres, B.A. 1989. Littoral zone use by post-breeding shorebirds on the Colville River Delta, Alaska. M.S. Thesis, Ohio State University.

Alaska Shorebird Group. 2008. Alaska Shorebird Conservation Plan. Version II. Anchorage: Alaska Shorebird Group.

Bart, J., S. Brown, B. Harrington, and R.I.G. Morrison. 2007. Survey trends of North American shorebirds: population declines or shifting distributions? Journal of Avian Biology 38:73-82.

Barta, Z., J.M. McNamara, A.I. Houston, T.P Weber, A. Hedenstrom, and O. Fero. 2008. Optimal moult strategies in migratory birds. Philosophical Transactions of the Royal Society B:363-211-229.

Brown, J.H. 1995. Macroecology. Chicago: University of Chicago Press.

Brown, J.H., and B.A. Maurer. 1989. Macroecology: the division of food and space among species on continents. Science 243: 1145-1150.

Butler, R.W., and G.W. Kaiser. 1995. Migration chronology, sex ratio, and body mass of Least Sandpipers in British Columbia. Wilson Bulletin 107:413-422.

Butler, R.W., G.W. Kaiser, and G.E.J. Smith. 1987. Migration chronology, length of stay, sex ratio, and weight of Western Sandpipers (*Calidris mauri*) on the south coast of British Columbia. Journal of Field Ornithology 58:103-111.

Callaghan, T.V., L.O. Bjorn, F.S.C.Chapin III, Y. Chernov, R. Torben, et al. 2005. Arctic Tundra and Polar Desert Ecosystems. In:.Arctic Climate Impact Assessment (ACIA). Cambridge University Press, Cambridge, UK, 1042 pp.

Chapin, F.S.C., III., S.R. Carpenter, G.P. Kofinas, C. Folke, W.C. Clark, et al. 2010. Ecosystem stewardship: sustainability strategies for a rapidly changing planet. Trends in Ecology and Evolution 25:241-249.

Connors, P.G. 1983. Distribution and biology of Semipalmated Sandpipers and Western Sandpipers in Alaska. RU-0172 report, Bodega Bay, California: Bodega Marine Laboratory.

Connors, P.G. 1984. Ecology of shorebirds in the Alaskan Beaufort littoral zone. In: R. Barnes, D.M. Shell, E. Ramirez, eds. The Alaskan Beaufort Sea: Ecosystems and environments. New York: Academic Press.

Connors, P.G., and R.W. Risebrough. 1977. Shorebird dependence on arctic littoral habitats. Annual Report, RU-0172, Outer Continental Shelf Environment Assessment Program. Boulder, CO: Bureau of Land Management/National Oceanic and Atmospheric Administration.

Connors, P.G., C.S. Connors, and K.G. Smith. 1981. Shorebird littoral zone ecology of the Alaska Beaufort Coast. Anchorage: Bureau of Land Management/National Oceanic and Atmospheric Administration, Outer Continental Shelf Environmental Assessment Program. Final Reports of Principal Investigators 23:295– 396.

Connors, P.G., J.P. Myers, and F.A. Pitelka 1979. Seasonal habitat use by Arctic Alaskan shorebirds. Studies in Avian Biology 2:101–111.

Gill, R.E., C.H. Handel, and P.C. Connors. 1985. Bird utilization of Peard Bay and vicinity. In: P.J. Kinney, ed. Environmental characterization and biological utilization of Peard Bay. Anchorage: Bureau of Land Management/National Oceanic and Atmospheric Administration, Outer Continental Shelf Environmental Assessment Program. Final Reports of Principal Investigators 35:244-323.

Gratto-Trevor, C.L., V.H. Johnston, and S.T. Pepper. 2001. Evidence for declines in Arctic populations of shorebirds. Bird Trends, Winter 2001:27-29.

Haig, S.M., D.W. Mehlman, and L.W. Oring. 1998. Avian movements and wetland connectivity in landscape conservation. Conservation Biology 12:749-758.

Hicklin, P. and C.L. Gratto-Trevor. 2010. Semipalmated Sandpiper (*Calidris pusilla*). In: A. Poole, ed. The Birds of North America Online. Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/006

Holmes, R.T. 1966a. Breeding ecology and annual cycle adaptations of the Red-backed Sandpiper (*Calidris alpina*) in northern Alaska. Condor 68:3-46.

Holmes, R.T. 1966b. Molt cycle of the Red-backed Sandpiper (*Calidris alpina*) in western North America. Auk 83:517-533.

Holmes, R.T. 1971. Latitudinal differences in the breeding and molt schedules of Alaskan Red-backed Sandpipers (*Calidris alpina*). Condor 73:93-99.

Holmes, R.T. 1972. Ecological factors influencing the breeding season schedule of Western Sandpipers (*Calidris mauri*) in subarctic Alaska. American Midland Naturalist 87:472-491.

Holmes, R.T. and F.A. Pitelka. 1998. Pectoral Sandpiper (*Calidris melanotos*). In: A. Poole, ed. The Birds of North America Online. Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/348

International Wader Study Group. 2003. Are waders world-wide in decline? Reviewing the evidence. Wader Study Group Bulletin 101/102:8-12.

Iverson, G.C., S.E. Warnock, R.W. Butler, M.A. Bishop, and N. Warnock. 1996. Spring migration of Western Sandpipers along the Pacific coast of North America: a telemetry study. Condor 98:10-21.

Johnson, O.W. and P.G. Connors. 2010. American Golden-Plover (*Pluvialis dominica*). In: A. Poole, ed. The Birds of North America Online. Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/201

Johnson, S.R., D.A. Wiggins, and P.F. Wainwright. 1993. Late-summer abundance and distribution of marine birds in Kasegaluk Lagoon, Chukchi Sea, Alaska. Arctic 46:212-1227.

Keppie, D.M. 2006. Context, emergence, and research design. Wildlife Society Bulletin 34:242-246.

Klima, J., and J.R. Jehl, Jr. 1998. Stilt Sandpiper (*Calidris himantopus*). In: A. Poole, ed. The Birds of North America Online. Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/341

Lanctot, R. B. and C. D. Laredo. 1994. Buff-breasted Sandpiper (*Tryngites subruficollis*). In: A. Poole, ed. The Birds of North America Online. Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/091

Lee, K. N. 1999. Appraising adaptive management. Conservation Ecology 3:3 [online] URL: http://www.consecol.org/vol3/iss2/art3/.

Lehnhausen, W.A., and S.E. Quinlan. 1981. Bird migration and habitat use at Icy Cape, Alaska. Anchorage: U.S. Fish and Wildlife Service, unpublished report. Available from Available at the Alaska Resources Library and Information Services. http://www.arlis.org.

Lyons, J.E. and S.M. Haig. 1995. Fat content and stopover ecology of spring migrant Semipalmated Sandpipers in South Carolina. Condor 97:427-437.

Macwhirter, B., P. Austin-Smith, Jr. and D. Kroodsma. 2002. Sanderling (*Calidris alba*). In: A. Poole, ed. The Birds of North America Online. Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/653

Martin, P.D., and C.S. Moiteret. 1981. Bird populations and habitat use, Canning River Delta, Alaska. Fairbanks: U.S. Fish and Wildlife Service. Available from U.S. Fish and Wildlife Service, Arctic National Wildife Refuge, 101 12th Avenue, Room 236, Fairbanks, Alaska 99701.

Moores, N., P. Battley, D. Rogers, M.N. Park, H.C. Sung, J. Van de Kam, and K. Gosbell. 2006 . Birds Korea – Australian Wader Study Group Saemangeum Shorebird Monitoring Program Report, 2006. Busan: Birds Korea.

Morrison, R.I.G., Y. Aubry, R.W. Butler, G.W. Beyersbergen, G.M. Donaldson, C.L. Gratto-Trevor, P.W. Hicklin, V.H. Johnston, and R.K. Ross. 2001. Declines in North American shorebird populations. Wader Study Group Bulletin 94:34-38.

Moskoff, W. and R. Montgomerie. 2002. Baird's Sandpiper (*Calidris bairdii*). In: A. Poole, ed. The Birds of North America Online. Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/661

Nettleship, D.N. 2000. Ruddy Turnstone (*Arenaria interpres*). In: A. Poole, ed. The Birds of North America Online. Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/537

Nol, E. and M.S. Blanken. 1999. Semipalmated Plover (*Charadrius semipalmatus*). In: A. Poole, ed. The Birds of North America Online. Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/444

Noskov, G.A., T.A. Rymkevich, and N.P. Iovchenko. 1999. Intraspecific variation of moult: adaptive significance and ways of realization. In: N.J. Adams and R.H. Slowtow, eds. Proceedings of the 22nd International Ornithological Congress, Durban, South Africa:544-563. Johannesburg: BirdLife South Africa.

O'Hara, P.D., D.B. Lank, and F.S. Delgado. 2002. Is the timing of moult altered by migration? Evidence from a comparison of age and residency classes of Western Sandpipers (*Calidris mauri*) in Panama. Ardea 90:61-70.

O'Reilly, K.M., and J.C. Wingfield. 1995. Spring and autumn migration in Arctic shorebirds: same distance, difference strategies. American Zoologist 35:222-233.

Paulson, D.R. 1995. Black-bellied Plover (*Pluvialis squatarola*). In: A. Poole, ed. The Birds of North America Online. Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/186

Payne, R.B. 1972. Mechanisms and control of moult. In: D.S. Farner and J.R. King, eds. Avian Biology, Vol. 5. New York: Academic Press.

Piersma, T. 1987. Hop, skip, or jump? Constraints on migration of arctic waders by feeding, fattening, and flight speed. Limosa 60: 185-194 (in Dutch).

Rubega, M.A., D. Schamel and D.M. Tracy. 2000. Red-necked Phalarope (*Phalaropus lobatus*). In: A. Poole, ed. The Birds of North America Online. Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/538

Sitters, H.P., and P.S. Tomkovich. 2010. Indicator #3: shorebirds – red knot. In: Arctic Biodiversity Trends 2010: selected indicators of change. Arctic Council, Conservation of Arctic Flora and Fauna Working Group. Available online at http://www.arcticbiodiversity.is/.

Skagen, S.K., and F.L. Knopf. 1993. Toward conservation of midcontinental shorebird migrations. Conservation Biology 7:533-541.

Skagen, S.K., and F.L. Knopf. 1994. Migrating shorebirds and habitat dynamics at a prairie wetland complex. Wilson Bulletin 106:91-105.

Spindler, M.A. 1979. Bird populations in coastal habitats, Arctic National Wildlife Range, Alaska: results of 1978 and 1979 aerial surveys. Fairbanks: U.S. Fish and Wildlife Service. Available from U.S. Fish and Wildlife Service, Arctic National Wildife Refuge, 101 12th Avenue, Room 236, Fairbanks, Alaska 99701.

Suryan, R.M., F. Sato, G.R. Balogh, K.D. Hyrenbach, P.R. Sievert, and K. Ozaki. 2006. Foraging destinations and marine habitat use of short-tailed albatrosses: a multi-scale approach using first-passage time analysis. Deep Sea Research Pt. II 53:245-261.

Takekawa, J.Y. and N. Warnock. 2000. Long-billed Dowitcher (*Limnodromus scolopaceus*). In: A. Poole, ed. The Birds of North America Online. Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/493

Taylor, A.R., R.B. Lanctot, A.N. Powell, F. Huettmann, D.A. Nigro, and S.J. Kendall. 2010. Distribution and community characteristics of staging shorebirds on the northern coast of Alaska. Arctic 63:451-467.

Thompson, C.W., and M. Leu. 1994. Determining homology of molts and plumages to address evolutionary questions: a rejoinder regarding emberizid finches. Condor 96:769-782.

Tracy, D.M., D. Schamel and J. Dale. 2002. Red Phalarope (*Phalaropus fulicarius*). In: A. Poole, ed. The Birds of North America Online. Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/698

Turner, M.G. 1989. Landscape ecology: the effect of pattern on process. Annual Review of Ecology and Systematics 20:171-197.

Warnock, N., and M.A. Bishop. 1998. Spring stopover ecology and migrant Western Sandpipers. Condor 100:456-467.

Warnock, N.D., and R.E. Gill. 1996. Dunlin (*Calidris alpina*). In: A. Poole, ed. The Birds of North America Online. Ithaca: Cornell Lab of Ornithology. Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/203; DOI:10.2173/bna.203.

Williams, T.D., N Warnock, J.Y. Takekawa, and M.A. Bishop. 2007. Flyway-scale variation in plasma triglyceride levels as an index of refueling rate in spring-migrating Western Sandpipers (*Calidris mauri*). Auk 124:886-897.

Wilson, W. H. 1994. Western Sandpiper (*Calidris mauri*). In: A. Poole, ed. The Birds of North America Online. Ithaca: Cornell Lab of Ornithology. Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/090; DOI:10.2173/bna.90.

Wu, J., and R. Hobbs (eds). 2007. Key Topics in Landscape Ecology. Cambridge: Cambridge University Press.

Yen, P.P.W., W.J. Sydeman, S.J. Bograd, and K.D. Hyrenbach. 2006. Spring-time distributions of migratory marine birds in the southern California Current: oceanic eddy associations and coastal habitat hotspots over 17 years. Deep Sea Research Pt. II 53:399-418.

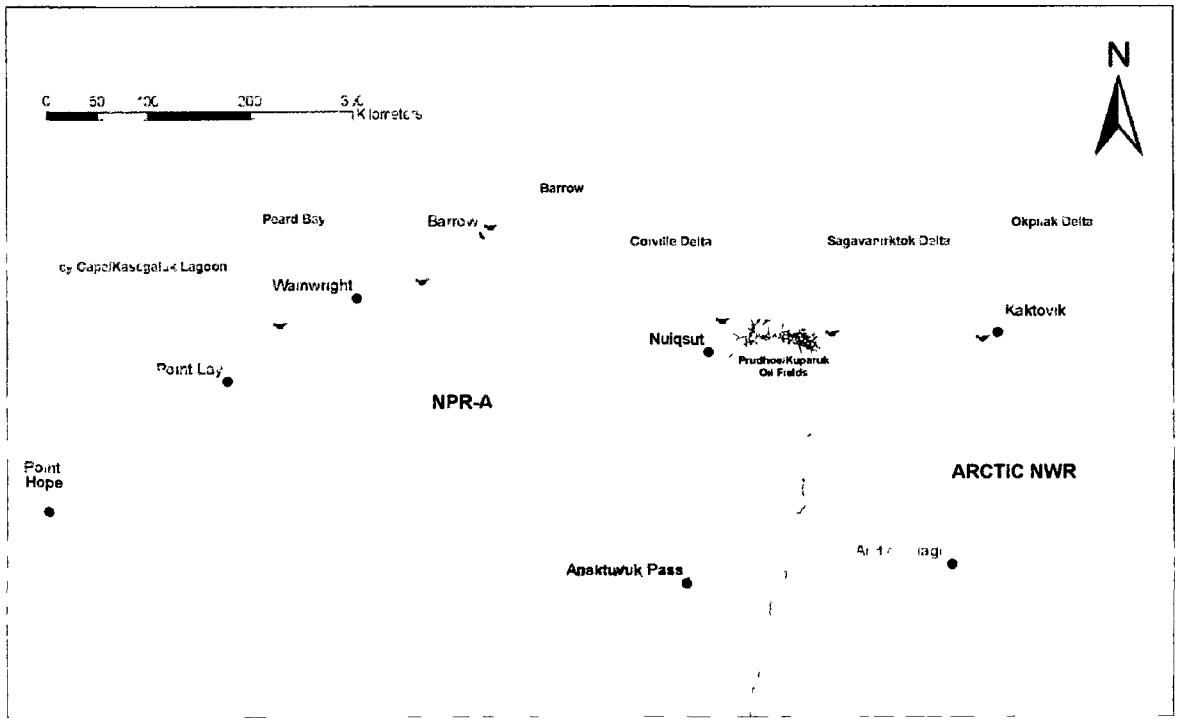

Figure 1.1. Map of study area: littoral zone of the Arctic Coastal Plain, Alaska. Yellow circles with shorebird symbol indicate locations of specific study sites used for this dissertation research in 2005-2006. Map courtesy of Philip Martin, U.S. Fish and Wildlife Service, Fairbanks AK.

Table 1.1. Characteristics of shorebird species common during the postbreeding period on the ACP of Alaska. North American population size and trend information taken from the Alaska Shorebird Conservation Plan, Version II (Alaska Shorebird Group 2008). BNA reference column gives the citation for the Birds of North America report for each species, which can be found online at http://bna.birds.cornell.edu.proxy.library.uaf.edu/bna.

Name	Scientific name	Breeding range in Alaska	Wintering range	Flyway	North American population size	Population trend	BNA reference
Black-bellied Plover	*Pluvialis squatarola*	coastal north and west	Americas	Pacific	50,000	stable	Paulson 1995
American Golden-plover	*Pluvialis dominica*	northern half	South America	Mississippi & Atlantic	200,000	decreasing	Johnson & Connors 2010
Semipalmated Plover	*Charadrius semipalmatus*	entire state	Americas	Pacific & Mississippi	150,000	stable	Nol & Blanken 1999
Ruddy Turnstone	*Arenaria interpres*	coastal north and west	Americas	Central Pacific & Pacific Americas	65,000	stable	Nettleship 2000
Sanderling	*Calidris alba*	ACP; rare	Americas	Pacific Americas	300,000	decreasing	Macwhirter et al. 2002
Semipalmated Sandpiper	*Calidris pusilla*	coastal north and west	Americas	Mississippi & Atlantic	2,000,000	decreasing	Hicklin & Gratto-Trevor 2010

Table 1.1 continued.

Western Sandpiper	*Calidris mauri*	coastal north and west	Americas	Pacific Americas	3,500,000	decreasing	Wilson 1994
Baird's Sandpiper	*Calidris bairdii*	northern half	South America	Mississippi	300,000	stable	Moskoff & Montgomerie 2002
Pectoral Sandpiper	*Calidris melanotos*	ACP	South America	Mississippi	500,000	stable	Holmes & Pitelka 1998
Dunlin	*Calidris alpina*	coastal north and west	East Asia/ Australasia	East Asian/ Australasian	500,000?	decreasing	Warnock & Gill 1996
Stilt Sandpiper	*Calidris himanotopus*	ACP	Americas	Mississippi	820,000	stable	Klima & Jehl 1998
Buff-breasted Sandpiper	*Tryngites subruficollis*	ACP	South America	Mississippi	30,000	decreasing	Lanctot & Laredo 1994
Long-billed Dowitcher	*Limnodromus scolopaceus*	coastal north and west	Americas	Pacific, Mississippi, & Atlantic	400,000	stable	Takekawa & Warnock 2000
Red Phalarope	*Phalaropus fulicaria*	ACP	offshore Americas	Pacific Americas	2,500,000	decreasing	Tracy et al. 2002
Red-necked Phalarope	*Phalaropus lobatus*	entire state	offshore Americas	Pacific Americas	1,250,000	decreasing	Rubega et al. 2000

2. DISTRIBUTION AND COMMUNITY CHARACTERISTICS OF STAGING SHOREBIRDS ON THE NORTHERN COAST OF ALASKA[1]

2.1. Abstract

Avian studies conducted in the 1970's on Alaska's Arctic Coastal Plain (ACP) indicated that coastal littoral habitats are important to arctic-breeding shorebirds for staging prior to fall migration. However, relatively little recent, broad-scale, or quantitative information exists on shorebird use of staging areas in this region. During the summers of 2005-2007, we conducted aerial surveys to locate possible shorebird concentration areas (based on relative shorebird abundance) in the littoral zone of the ACP from the southwest end of Kasegaluk Lagoon on the Chukchi Sea to Demarcation Bay in the Beaufort Sea. These surveys identified persistent within- and between-year concentrations of staging shorebirds at Peard Bay, Pt. Barrow/Elson Lagoon, Cape Simpson, and Smith Bay to Cape Halkett. Among river deltas in the Beaufort Sea, the Sagavanirktok and Kongakut deltas had large concentrations of staging shorebirds. We also collected data on shorebird community characteristics, staging phenology, and habitat use in 2005 and 2006 by conducting land-based surveys at six camps: Kasegaluk Lagoon, Peard Bay, Pt. Barrow/Elson Lagoon, Colville Delta, Sagavanirktok Delta, and Okpilak Delta. The shorebird community was more even and diverse (evenness E and Shannon Weiner *H'*)

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along the Beaufort Sea compared to the Chukchi Sea and in 2005 versus 2006. Staging phenology varied by species and location, and differed than that reported in previous studies for several species. Our results suggest the existence of three foraging habitat guilds among the shorebird species observed in this study: gravel beach, mudflat, and salt marsh/pond edge. These foraging associations appear to be conserved through time when compared to data collected in the mid-1970's. Results from this research will be useful for land managers to monitor the effects of changing environmental conditions and human activity on shorebirds and their habitats in arctic Alaska.

Key words: Shorebird, postbreeding, staging, distribution, community composition, phenology, habitat selection, aerial survey, climate change, industrial development, Arctic Coastal Plain, Alaska

2.2. Introduction

At least twenty species of shorebirds stage in littoral habitats on the northern coast of Alaska (the Arctic Coastal Plain [ACP]) prior to fall migration (Connors, 1984), where they acquire fat reserves necessary for long distance flights. Although there is a considerable body of literature on stopover ecology of shorebirds during migration (e.g., Holmgren et al., 1993; Skagen and Knopf, 1993; Lyons and Haig, 1995), less research has been conducted on shorebirds staging prior to migration. Numerous studies have

addressed shorebird use of ACP littoral habitats, but many of these are relatively dated, somewhat anecdotal in nature, or focused on a single or few study areas, and the data are not readily available in the published literature (e.g., Johnson, 1978; Spindler, 1979; Lehnhausen and Quinlan, 1981; Gill et al., 1985; Andres; 1989; Johnson et al., 1993). In addition, few studies have been designed specifically to examine the distribution of small shorebird species, with most studies conducted ancillary to larger, more obvious species (such as waterfowl). Much of what is known regarding shorebird populations staging on the coast of the ACP resulted from research done during the Outer Continental Shelf Environmental Assessment Program (OCSEAP) in the mid-1970's (Connors et al., 1979; Connors et al., 1981; Connors, 1984). These studies found that shorebirds moved from tundra breeding sites to coastal littoral staging areas as the summer progressed. Birds tended to aggregate in littoral areas and were found in greater densities than during the breeding season, underscoring the importance of coastal zones in the life cycles of migratory shorebirds in northern Alaska.

A variety of studies have identified shorebirds as an avian group highly susceptible to human-induced disturbance (Burger, 1981; Smit and Visser, 1993; Burger et al., 2007). Global populations of shorebirds are in decline (Brown et al., 2001; International Wader Study Group, 2003), including eleven species that regularly breed and stage on the ACP. Nine of these have been classed as highly imperiled or of high concern at the global or North American level (U.S. Shorebird Conservation Plan, 2004). The International Wader Study Group (2003:10) concluded that "...reduced suitability of

staging sites [has] major implications for the survival and reproduction of [long-distance] migrants," and that "'virtual habitat loss' can occur...as a consequence of poor management such as that which arises from unsustainable exploitation of natural resources, disturbance, and other local perturbations." Industrial development is increasing in scope and intensity across the Arctic (Gilders and Cronin, 2000; National Research Council, 2003), creating the potential for disturbance, habitat modification, and contaminant spills to impact a large segment of a species' population, especially when species become aggregated in coastal areas after the breeding season. In addition, increases in surface air temperature leading to rapid ecological change are believed to be amplified at higher latitudes (Sereze et al., 2000; IPCC, 2001; Holland and Bitz, 2003). Accelerated ecological change in a warming Arctic may add to the potential effects of industrial development through processes such as sea level rise, coastal erosion and inundation, and altered sediment transport and deposition patterns (ACIA, 2005). These processes may modify the spatial or temporal availability of littoral habitats suitable for staging shorebirds. Changes in the timing of insect emergence patterns could also alter the phenology of the staging period for postbreeding shorebirds (Tulp and Shekkermann, 2008; Van der Jeugd et al., 2009).

Information on current distribution, relative abundance, phenology, and habitat preferences is critical for predicting the effects of changing Arctic conditions on the location and persistence of staging shorebird aggregations on the northern Alaska coast (Sereze et al., 2000; McCarty, 2001; Hinzman et al., 2005; Maclean et al., 2008). Also,

comparing current shorebird diversity and abundance with previous shorebird community data could aid in setting conservation targets and priorities if maintenance of historic species composition and diversity patterns is a goal (Stein and Davis, 2000). Documenting habitat use and selection by postbreeding shorebirds is important for understanding large-scale patterns of distribution and abundance, and for predicting effects of ecological change that may vary by habitat type. Our overall objective was to document for the postbreeding staging period on the ACP coast: (1) geographic distribution of shorebirds on a large scale, including temporal variation, and (2) community characteristics, species composition, phenology, and habitat selection for the staging shorebird community at six specific sites on the ACP coast. We also compare our data to previous work conducted between 1975 and 1993 to determine what changes may have already occurred in postbreeding shorebird ecology on the northern Alaska coast.

2.3. Study area

Our study area was the coastline and major river deltas of the Chukchi and Beaufort Seas between the south end of Kasegaluk Lagoon and Demarcation Point (the Alaska/Canada border; Fig. 2.1). Littoral habitats along this portion of the ACP include brackish water mudflats and marsh; low-lying saline tundra; mud and gravel shores of sloughs, river deltas, and lagoons; and gravel mainland and barrier island beaches. Tidal influence in the absence of storms is <30 cm vertical fluctuation, but wind-driven tidal intrusion is

common during the ice-free period (July-September), resulting in brackish habitats well above normal high tide lines (Connors et al. 1979).

We flew aerial surveys across the study area to collect information on geographic distribution of staging shorebirds. We also established six ground camps located at (Fig. 2.1): Kasegaluk Lagoon (70.301°N, 161.888°W; operated 2006 only), Peard Bay (70.812°N, 158.323°W), Pt. Barrow/Elson Lagoon (71.290°N, 156.788°W), Colville Delta (70.473°N, 150.564°W), Sagavanirktok Delta (70.291°N, 148.202°W in 2005; moved to 70.246°N, 147.832°W in 2006), and Okpilak Delta (70.080°N, 144.011°W). The ground camp locations were selected opportunistically based on (1) the presence of either a large lagoon system (Kasegaluk, Peard Bay, Pt. Barrow/Elson Lagoon) or a large river delta (Colville, Sagavanirktok, Okpilak), both of which might support large numbers of staging shorebirds, (2) the potential for logistical support from other project collaborators for conducting work at the site, and (3) the ability to access the sites with fixed-wing aircraft or boats for deployment of personnel and equipment.

2.4. Methods

2.4.1. Geographic distribution from aerial surveys

To obtain a broad-scale perspective on staging shorebird distribution through time, we conducted aerial surveys of the ACP coast from 2005-2007. Surveys comprised counts of birds within a fixed-width transect along the land/sea interface of the coastline. This

survey band comprised the vast majority of the ACP littoral zone, defined as the region from the lowest tide level to the highest storm-driven water line (Connors et al., 1981). The area covered during each survey varied for logistical reasons and because weather prohibited the extent and number of flights (Table 2.1). From 7-16 August 2005, we conducted a single survey of the ACP coastline between the south end of Kasegaluk Lagoon and Demarcation Point with a Robinson R-44 helicopter at an altitude of approximately 15 m and a cruising speed of 95-115 km/hr (depending on wind speed). The front left biologist identified and counted birds within 150 m to the left of the centerline of the aircraft (looking from the edge of the water inland), while the rear left biologist recorded data. We recorded all shorebirds within belt transect sections designated by GPS locations recorded every two minutes. The use of two-minute intervals enabled calculation of bird densities on a per-time period, per-transect, or per-habitat basis (Johnson et al., 1993). Between 22 July and 27 August 2006, we conducted four surveys of the ACP coast in a Bellanca Scout fixed-wing aircraft, flying at an altitude of approximately 15 m and a cruising speed of 130-170 km/hr. Shorebird observations were recorded by a single observer from the rear seat of the plane, looking on one side of the aircraft from the land/sea interface to 150 m inland. We used the GPSVOX voice-recorder interface program developed by John Hodges (U.S. Fish and Wildlife Service, Juneau, AK) that records a GPS location and audio file for each observation; these were later transcribed into geo-referenced data points. In addition to the coastline surveys, we surveyed all major river deltas in 2006 by recording birds along

transects spaced 1 km apart that ran perpendicular to the coastline to the inland extent of salt marsh or mudflat habitat. In 2007, we utilized the same fixed-wing aircraft survey techniques as in 2006 but limited our surveys to only the Arctic National Wildlife Refuge coast from the Canning River to Demarcation Point because this area was infrequently surveyed in 2006.

We divided the ACP coast into four main regions to analyze the aerial survey data: 1) Chukchi: the south end of Kasegaluk Lagoon to the Chukchi Sea side of Pt. Barrow, 2) Western Beaufort: the Elson Lagoon side of Pt. Barrow to the west side of the Colville River delta, 3) Central Beaufort: Colville River delta to the West Canning River delta, and 4) Arctic Refuge: the West Canning River delta to Demarcation Point (Fig. 2.1). We then created sub-regions (containing similar distribution of habitat types) within each of the four larger regions. We chose to divide the analysis this way because we believed that comparing shorebird abundance across the entire ACP coast would potentially disvalue concentration areas that may have been locally important to birds moving along the coastline during the staging period. The four regions we delineated represent significantly different habitats: the Chukchi coast is mostly gravel beach and exposed shorelines, the Western Beaufort consists of many coastal lakes, the Central Beaufort contains the oil fields and is mostly high bluff habitat, and the Arctic Refuge region consists of many small (and some larger) river deltas. If all these regions were available to choose from at the same time birds might prefer some over others, but the fact that a bird must fly from one point to another in a linear pattern likely constrains its

choice of staging areas at any given time. Additionally, development decisions on the ACP are likely to be made on a relatively local level (e.g., an oil platform may be put at this delta or the next one over), thus it is valuable to examine where shorebirds choose to stage relative to other nearby areas.

To show shorebird distributions for the 2005 helicopter survey, we imported the coordinates of the endpoints of each two-minute flight interval (representing ca. 3.5 km on the ground) and the total number of birds within each interval into ArcMap 9.1 (ESRI Inc., 2005). Because the exact number of birds counted within each interval was not available (these detailed data were lost), we report the data in categories of <50, 50-99, 100-499, 500-999 and ≥ 1000 for each flight interval. Then, we overlaid the 2006-2007 fixed-wing data on top of the 2005 intervals to obtain the number of birds within each two-minute interval for each survey period in 2006 and 2007. We averaged these per-interval counts for each sub-region in each survey period. There were a total of four survey periods in 2006 and one in 2007 (Table 2.1). For the purpose of delineating important staging areas, we defined a "shorebird concentration area" as sub-region with mean per-interval counts of birds at least 50% higher than other sub-regions within that region during the same time period. We then compared results from the single 2005 helicopter survey to the results from the third 2006 fixed-wing survey to assess basic similarities across years in abundance and distribution. These two surveys were conducted during approximately the same time period (August 7-16 in 2005 vs. August 9-17 in 2006; Table 2.1). We did not correct for the differences in aircraft used between

the two years because we felt that the faster speed of the fixed-wing aircraft was balanced by the greater disturbance potential of the helicopter (Ward et al., 1999), thus detectability from both aircraft was similar.

We considered river deltas along the Beaufort Sea coast separately. These areas comprise a distinct habitat demarcated by the location of the active floodplain of the river, and the potential staging habitat is much wider than along a non-deltaic coastline. Surveying deltas required us to fly linear transects perpendicular to the coast, rather than flying a single linear survey that paralleled the coastline as we did in non-delta areas. We determined the total number of shorebirds observed on each river delta rather than per-interval counts since we did not have categorical 2005 data for the deltas which would have constrained our ability to estimate abundance in 2005 and thus compare patterns between years. We considered a delta to be a "shorebird concentration area" if it had total counts of shorebirds at least 50% higher than other deltas during the second 2006 survey, when all deltas were surveyed over a relatively short period of time. This definition of importance is less rigorous than for coastal sub-regions (see above) because we had less comparative data for the deltas.

All aerial survey data are reported as raw count data, uncorrected for detectability. We attempted to use distance sampling analysis methods (implemented in Program DISTANCE; Thomas et al., 2006) to estimate detection rates for shorebirds from aerial surveys but found that our methodology violated several key assumptions of this analysis method: (1) shorebirds exhibited evasive movement in response to the aircraft and thus

were not detected at their initial location, and (2) birds that flew under the aircraft were not observed, thus detection on the transect line was far from 100% (Buckland et al., 2001). We stress that our emphasis is on large-scale distribution of staging shorebirds rather than on exact density or abundance in any one location. We were unable to reliably identify individual species from the air, so we report distribution and abundance patterns for all shorebirds combined.

2.4.2. Shorebird community characteristics from ground camps

During 2005 and 2006, we conducted a series of surveys at each of the ground camps to assess species composition, staging phenology, and habitat use of staging shorebirds. We established nine 1 km transects within a 10 km diameter study area at each ground camp. Transects were not located randomly, but rather were located where birds were seen or believed to be foraging, and, if possible, to sample each of four habitat types: gravel beach, mudflat (silt barren), pond edge, and salt marsh. The proportions of each habitat varied with location and thus were not sampled equally across all camps. Gravel beach was typically found on exposed shorelines along the Chukchi Sea, and along barrier islands in the Beaufort Sea. Mudflat consisted of open riverine silt deposits or dried pond/lake basins. Pond edge was comprised of shallow water, mud, and sand found along the border of small ponds, lakes, or lagoons. Salt marsh was characterized by low-growing, saline tolerant vegetation and periodically inundated substrate. Transects at each camp were surveyed by a single observer on foot once every three days throughout

the field season (24 July-30 August 2005, 15 July-4 September 2006), although exact survey dates varied slightly by camp. We recorded species, group size, age composition (number of adult and juvenile birds), distance from transect, and habitat type occupied for all shorebirds observed on either side of each transect, out to 300 m. To characterize available habitat for later assessment of habitat selection, we also recorded the proportion of each of the four habitat types along each transect by measuring the length of the transect that ran through each habitat type.

2.4.2.1. Species richness, evenness, and diversity

We quantified shorebird communities by calculating (1) species richness (total number of species observed), (2) evenness (E, abundance of each species relative to others in the community), and (3) the proportion of the total community belonging to each species (*H'*, Shannon-Wiener diversity index) at each ground camp in each year (Pielou, 1974). To obtain measures of precision for evenness and diversity, we performed a series of 100 bootstrap simulations of the observed count data for each species and used their standard errors for subsequent comparisons of geographic variation (Kowalewski et al., 2006). We tested whether species evenness and diversity varied by camp with one-way ANOVA (Proc GLM, SAS 9.1, SAS Institute, Inc., 2003) and by coast (Chukchi vs. Beaufort) with t-tests (Proc TTEST, SAS 9.1, SAS Institute, Inc., 2003), using Satterthwaite's approximation for degrees of freedom because sample sizes were not equal across camps (Snedecor and Cochran, 1980:97).

2.4.2.2. Species composition and phenology

To assess species composition (relative abundance of shorebird species at each site) and phenological patterns in the ground transect data, we calculated the number of individuals of each species recorded during each transect survey, after assigning all data to survey periods that were consistent across camps. These survey periods were as follows: 1: 17-19 July, 2: 20-22 July, 3: 23-25 July, 4: 26-28 July, 5: 29-31 July, 6: 1-3 August, 7: 4-6 August, 8: 7-9 August, 9: 10-12 August, 10: 13-15 August, 11: 16-18 August, 12: 19-21 August, 13: 22-24 August, 14: 25-27 August, 15: 28-30 August, and 16: 31 August-2 September. Survey periods were the same in 2005 as 2006, except that surveys were not conducted during the first two periods nor the last period in 2005. We do not present shorebird densities because some habitats were best estimated as a linear density and others as an areal density, making such comparisons impractical and misleading. Reporting actual counts rather than densities also facilitated comparisons with previous studies, although detectability is unknown in both these studies and ours.

To place the phenology data in context, we used snow depth data from NOAA's National Weather Service Barrow Post Rogers Airport station, available online from the National Climatic Data Center at http://www4.ncdc.noaa.gov/cgiwin/wwcgi.dll?wwDI~StnSrch~StnID~20022476. We used as the snow melt date for a given year the date that snow depth at Barrow was first reported to be a "trace" instead of a number of inches. We chose this measurement because more than ambient temperature, the amount of snow covering tundra nesting

habitat appears to impact breeding behavior of shorebirds (ACIA, 2005; Meltofte et al., 2008).

2.4.2.3. Habitat selection

Habitat use is said to be selective if habitats are used disproportionately to their availability (Alldredge and Griswold, 2006). We used the ground transect data to create resource selection functions (RSF; Manly et al., 2002) in TreeNet (Salford Systems, 2003) to assess habitat selection for twelve relatively common shorebird species: American golden-plover (*Pluvialus dominica*), black-bellied plover (*P. squatarola*), dunlin, long-billed dowitcher (*Limnodromus scolopaceus*), pectoral sandpiper (*C. melanotos*), red phalarope, red-necked phalarope, ruddy turnstone (*Arenaria interpres*), sanderling (*C. alba*), semipalmated sandpiper, stilt sandpiper (*C. himanotopus*), and western sandpiper. TreeNet is a non-parametric data mining and modeling program that constructs additive regression trees by sequentially fitting a simple parameterized tree function at each iteration (Friedman, 2001; Craig et al., 2009). All species datasets entered into TreeNet were randomly split into 90% training data and 10% testing data for model accuracy assessment. For increased accuracy a subset of the training data was randomly selected without replacement and used in place of the full training set to compute the model update at each step (stochastic gradient boosting; Friedman, 2001). For each species, we examined the relative importance of habitat type, ground camp, season (early: 15-31 July, mid: 1-15 August, or late: 16 August to end of field season), and year in determining the ratio of used vs. available habitat. We considered the number

of birds (by species) counted in each habitat type/camp/season/year combination as a metric of habitat used, and the proportion of habitats across each of the nine transects within a camp as habitat availability. We present results of the TreeNet analysis as partial dependence plots, which allow visualization of the effect of the individual predictor variable (habitat category) on the modeled response (in this case the resource selection ratio) after accounting for the average effect of all other multivariate predictors (in this case ground camp, season, and year; Friedman, 2001; Hochachka et al., 2007). The greater the absolute partial dependence values for a given predictor, the more dependent the response is on variation within that predictor. For a given species, positive partial dependence values for a habitat category indicate selective use of that habitat; negative values indicate selection against that habitat. Because ground camps and transects were not randomly located, we recognize that our results cannot be extended beyond the area directly sampled by our transects without further evaluation data.

All shorebird survey activities for this project were conducted under a University of Alaska Fairbanks Institutional Animal Care and Use Committee protocol (#04-31).

2.5. Results

2.5.1. Geographic distribution from aerial surveys

2.5.1.1. Within years

In 2005, we found shorebird concentration areas (defined as a sub-region with mean per-interval counts of birds at least 50% higher than other sub-regions within that region during the same time period) at Kasegaluk Lagoon N and Peard Bay in the Chukchi region (Fig 2.2, first panel); Pt. Barrow/Elson Lagoon, Cape Simpson, and Smith Bay to Cape Halkett in the Western Beaufort region (Fig 2.2, second panel); and at numerous lagoons within the Central Beaufort and Arctic Refuge regions in 2005 (Fig. 2.2, third and fourth panels).

In 2006, relative shorebird abundance varied by sub-region and across surveys, although overall distribution patterns were similar to those observed in 2005. Peard Bay had higher per-interval counts than all other sub-regions in the Chukchi region during the first three surveys. In contrast, the sub-regions to either side of Peard Bay had high counts of birds during the fourth survey (Fig. 2.2, first panel). The Western Beaufort region had higher per-interval counts than any other region in the 2006 surveys, with Pt. Barrow/Elson Lagoon, followed by Cape Simpson, having more birds than any other subregion across the ACP coast. Within the Western Beaufort region, however, Admiralty Bay and the west side of Harrison Bay had lower counts of birds (Fig. 2.2, second panel). Overall, the Central Beaufort region had the lowest per-interval counts of

shorebirds of any region for all 2006 surveys, particularly for the fourth survey when almost no shorebirds were observed (Fig. 2.2, third panel). Within-season patterns were more difficult to discern for the Arctic Refuge region because only the first two surveys were completed in 2006 due to poor weather conditions. Per-interval shorebird counts during the second survey were generally higher than those recorded during the first survey, especially for the Beaufort Lagoon sub-region which was much higher (Fig. 2.2, fourth panel).

2.5.1.2. Between years

Based on a comparison of the 2005 survey results with those from the third 2006 survey, Peard Bay had consistently higher per-interval counts of staging shorebirds than other sub-regions of the Chukchi region in both years. In the Western Beaufort region, Pt. Barrow/Elson Lagoon and the Cape Simpson area had the highest counts of staging birds in both years, while Smith Bay to Cape Halkett had moderate counts of staging birds in both years. We observed few concentrations of staging shorebirds in the Central Beaufort region in either year. We were unable to survey the Arctic Refuge region in 2006 during the same time as we flew the 2005 helicopter survey in 2005. However, we can make a comparison between the second fixed-wing survey of 2006 and our single survey of 2007 conducted in the Arctic Refuge region (August 6-7 in 2006 and August 7-8 in 2007; Table 2.1). Camden Bay had higher counts of staging shorebirds than other sub-regions of the Arctic Refuge coast (excluding river deltas) in 2007, while Beaufort Lagoon had at least two times as many shorebirds during the second survey in 2006 than

any other lagoon in either year. However, neither area showed consistently high shorebird numbers across years. Demarcation Bay had low counts of shorebirds in both 2006 and 2007.

2.5.1.3 . River deltas

In terms of total number of birds observed, the Sagavanirktok and Kongakut deltas had particularly high counts during the second survey in 2006 (Fig. 2.3), which qualified them as shorebird concentration areas under our definition. We were only able to examine between-year data for the Arctic Refuge deltas. Between years, total numbers for the Jago and Kongakut deltas during the second survey in 2006 were substantially higher than those recorded on the same deltas during the 2007 survey, even though these surveys took place over the same time period in both years.

2.5.2. Shorebird community characteristics from ground camps

2.5.2.1. Species richness, evenness, and diversity

Generally, species richness, evenness, and diversity were higher in 2005 than in 2006 (Table 2.2). In both years, species richness was lowest at the Peard Bay and Sagavanirktok camps, and highest at the Pt. Barrow/Elson Lagoon, Colville Delta, and Okpilak Delta camps. Richness at Kasegaluk Lagoon was also low in 2006 (the only year for that camp). Species evenness (2005 E: $F = 49588.6$, df = 4, $P < 0.001$; 2006 E: $F = 2094510$, df = 5, $P < 0.001$) and diversity (2005 H': $F = 72725.9$, df = 4, $P < 0.0001$; 2006 H': $F = 1674642$, df = 5, $P < 0.0001$) across ground camps varied significantly

within each year, although there was not a consistent pattern across space or time (Table 2.2). Therefore, we grouped camps located along each coast (Chukchi vs. Beaufort Sea) and analyzed these regions for richness, evenness, and diversity. We included Pt. Barrow/Elson Lagoon in the Chukchi coast region because the habitat is mainly gravel beach, making the camp more similar to the Chukchi camps than to the Beaufort camps located at river deltas. Species richness did not differ between the Beaufort or Chukchi coasts in either year (2005: $t = 0.52$, $P = 0.32$; 2006: $t = 0.16$, $P = 0.44$). The Beaufort coast had greater evenness and diversity in both 2005 and 2006 than did the Chukchi coast, although the difference in evenness between the coasts in 2006 was only marginally significant (Table 2.2; significance of difference between 2005 and 2006 evenness and diversity indicated by overlap of bootstrapped 95% confidence intervals).

2.5.2.2. Species composition

Overall, the postbreeding shorebird community was comprised of three species (semipalmated sandpiper, dunlin, and red-necked phalarope) common to all locations, and two species (western sandpiper and red phalarope) that were common on the Chukchi coast but declined in relative abundance going east along the Beaufort coast (Table 2.3). Red phalaropes and dunlin were found in large numbers (>3000 and >1000 individuals, respectively) in several different survey periods, whereas semipalmated sandpipers and red-necked phalaropes were found in intermediate numbers (~300 individuals). Western sandpipers were the least common species comparatively. For all of these common species except dunlin, juveniles (HY) far outnumbered adults (AHY) on our transects; for

dunlin the reverse was true (Table 2.3). Ten other species (American golden-plover, Baird's sandpiper [*Calidris bairdii*], black-bellied plover, buff-breasted sandpiper [*Tryngites subruficollis*], long-billed dowitcher, pectoral sandpiper, ruddy turnstone, sanderling, semipalmated plover [*Charadrius semipalmatus*], and stilt sandpiper) were present at some or all camps in each year, but not more than ~300 individuals were observed at any one camp in a given year (Table 2.4). Long-billed dowitchers were more common on the Chukchi than the Beaufort coast, whereas black-bellied plovers, American golden-plovers, and stilt sandpipers were more common on the Beaufort than the Chukchi coast. Pectoral sandpipers were present at all camps in both years. Sanderlings and ruddy turnstones were more abundant at some camps than at others, with no particular geographic pattern. Baird's sandpipers, buff-breasted sandpipers, and semipalmated plovers were relatively rare at all camps. For all less common species, juveniles outnumbered adults on our transects.

2.5.2.3. Phenology

Semipalmated sandpipers were present at all camps only early in the staging period (Fig. 2.4). Peak abundance of juveniles occurred during 29 July-3 August on the Chukchi coast and during 4-9 August on the Beaufort coast; juveniles were mostly absent after 7-9 August on the Chukchi coast and 10-12 August on the Beaufort coast. Peak numbers of adults preceded those of juveniles by approximately six days at most camps; adults were mostly absent from our transects after 29-31 July.

Dunlin tended to be present over a longer portion of the staging period than other species (Fig. 2.4). Peak abundance was earliest at Kasegaluk Lagoon (26-28 July) and latest at the Okpilak Delta (31 August-2 September), although there was not a clear temporal trend between these sites. Peak numbers of adult dunlin were observed earlier than those of juvenile dunlin at most camps, but both age groups were present until the end of the field season. Within each camp, the periods of peak abundance for both age groups were similar.

For red-necked phalaropes, the period of peak abundance was relatively short at the Kasegaluk Lagoon, Peard Bay, and Okpilak camps, and longer at the Pt. Barrow/Elson Lagoon, Colville Delta, and Sagavanirktok Delta camps (Fig. 2.4). Peak abundance of juveniles occurred between 26-28 July at the Kasegaluk Lagoon camp and 13-15 August at Pt. Barrow/Elson Lagoon. There was no clear trend in date of peak abundance from east to west. Adults peaked in abundance up to twelve days in advance of juveniles, and were absent from the transects before juveniles at most camps.

Red phalaropes were relatively abundant throughout most of the staging period, especially at the Peard Bay and Pt. Barrow/Elson Lagoon camps (Fig. 2.4). Peak numbers of juveniles occurred between 1-6 August at all four camps where they were recorded, thus there was no clear trend in date of peak abundance from east to west. Adults and juveniles peaked in abundance at approximately the same time at most camps, although adults were absent from the transects prior to juveniles.

The peak of abundance for western sandpipers was 13-15 August at all camps, thus there was no trend in date of peak abundance from west to east (Fig. 2.4). This species was present at Chukchi Sea staging areas after the beginning of August for a relatively long period of time (especially in Barrow) compared to semipalmated sandpipers, a similar species. Very few adult western sandpipers were observed except at Kasegaluk Lagoon, where adults peaked in abundance up to three weeks in advance of juveniles, and were absent from the transects prior to juveniles.

Black-bellied plovers, American golden-plovers, pectoral sandpipers, and ruddy turnstones were present sporadically throughout the staging period at most camps. Baird's sandpipers, buff-breasted sandpipers, and semipalmated plovers were mostly observed during the first half of the staging period, while stilt sandpipers were mostly observed during the middle of the staging period. Sanderlings were mostly recorded during the second half of the staging period, except for a small pulse of individuals early in the staging period at Peard Bay. Long-billed dowitchers exhibited a distinct short pulse of abundance late in the staging period that was particularly evident at the Kasegaluk Lagoon and Peard Bay camps.

The snow melt date for 2005 was 28 May, and for 2006 was 7 June. The ten-year average for 2000-2009 was 28 May, while the five-year averages were 24 May for 2000-2004 and 1 June for 2005-2009.

2.5.2.4. Habitat selection

We detected three distinct patterns in species-habitat associations (which we termed foraging guilds) at our six ground camps (Fig. 2.5). Black-bellied plovers, red phalaropes, ruddy turnstones, and sanderlings selected for gravel beaches, whereas dunlin and semipalmated sandpipers strongly selected for mudflats. American golden-plovers, long-billed dowitchers, pectoral sandpipers, and western sandpipers selected for salt marshes, although three of these species (long-billed dowitchers, pectoral sandpipers, and western sandpipers) also selected for pond edge, which was often interspersed with salt marsh across our study site. Stilt sandpipers, while not widely distributed or numerous across our study area, also selected for pond edge where they were locally present, mostly east of the Colville delta. Red-necked phalaropes were the only species that did not fit clearly into a foraging guild: they showed approximately equal selection for gravel beach and pond edge.

2.6. Discussion

2.6.1. Geographic distribution from aerial surveys

Based on research done in the late 1970's as part of the Outer Continental Shelf Environmental Assessment Program (OCSEAP; Connors et al., 1981), we expected that staging shorebird distribution across the ACP coast would be non-uniform. Consistent with this expectation, we found shorebird concentration areas across years during aerial

surveys at Peard Bay, Pt. Barrow/Elson Lagoon, Cape Simpson, and between Smith Bay and Cape Halkett, whereas along other areas of the coastline few or no shorebirds were observed during our surveys. In addition, we found concentrations of shorebirds at the Sagavanirktok and Kongakut river deltas. Below, we compare our aerial survey results to those reported by previous investigators for areas found to be shorebird concentration areas in our study or by others. We present this information in geographic order from west to east across the ACP (see Fig. 2.1). To facilitate comparisons, we converted our per-interval count data to linear densities (birds/km) by dividing by 3.5 km (the approximate length of a two-minute interval flown in an R-44 helicopter).

2.6.1.1. Kasegaluk Lagoon

Although we did not find Kasegaluk Lagoon to be a shorebird concentration area across years, Johnson et al. (1993) reported large numbers of shorebirds across the entire lagoon during aerial surveys from 1989-1991, with densities of unidentified small shorebirds averaging between 4.4 (1989) and 45.5 (1991) birds/km. Peak counts of small shorebirds in each year were 4000 in 1989, 8000 in 1990, and 29 000 in 1991. Our peak counts of shorebirds during the 2006 surveys ranged from 39-1561 individuals per survey, and linear densities (averaged across all surveys) were approximately 2.0 birds/km in the south part of the lagoon and 0.9 birds/km in the north part. Given the historically high numbers of birds in this sub-region, Kasegaluk Lagoon may merit further investigation as a concentration area for shorebird staging/migration.

2.6.1.2. Peard Bay

Connors et al. (1981) listed Peard Bay as a sensitive concentration area for staging shorebirds due to its extensive gravel spit/beach habitat favored by phalaropes. Gill et al. (1985) conducted aerial shoreline surveys at Peard Bay from July to September 1983, and recorded a linear density of 0.8 shorebirds/km (mostly red phalaropes) on 10 August 1983. We observed approximately 2.5 shorebirds/km (mostly phalaropes) during our aerial survey on 9 August 2006. Connors and Risebrough (1978) and Gill et al. (1985) found that densities of shorebirds at Peard Bay were lower than densities at Icy Cape (in Kasegaluk Lagoon). In contrast, we found that densities of shorebirds at Peard Bay were higher than those at Kasegaluk Lagoon in all of our surveys. Gill et al. (1985) considered Peard Bay to represent a transition zone between estuarine systems typical of the Arctic coast and those typical of subarctic areas to the south. If this transitional habitat is related to food availability, Peard Bay may attract birds migrating south from the Beaufort coast as the first subarctic staging area on the Chukchi Sea. Birds staging at Peard Bay may then bypass Kasegaluk Lagoon, located only 80 miles southwest of Peard Bay along the Chukchi coast. A warming trend in the Arctic may increase the possibility that Peard Bay serves as a subarctic staging site, resulting in more individuals skipping Kasegaluk Lagoon.

2.6.1.3. Pt. Barrow/Elson Lagoon

We recorded the highest density (38.4 birds/km) of all surveyed regions (excluding deltas) at Pt. Barrow/Elson Lagoon during the third fixed-wing survey in

2006. Counts of birds in this sub-region were comparatively high in 2005 and during the other 2006 surveys as well. Connors et al. (1981) considered both Pt. Barrow and the Plover Islands (extending southeast from Pt. Barrow; Fig. 2.1) to be concentration areas for staging shorebirds during the OCSEAP study, and surmised that the extensive gravel spits and barrier islands of this area were attractive to staging shorebirds, particularly phalaropes.

2.6.1.4. Cape Simpson

The Cape Simpson sub-region had a peak density of 36.9 birds/km during the third survey in 2006, which was the second-highest density we observed during our aerial surveys. However, there are no other comparative data on staging shorebird abundance in this sub-region. The Cape Simpson area (particularly at Tangent Point, circled on Fig. 2.2b) is characterized by many small- to medium-sized lakes near the coastline, many of which show evidence of being breached by salt water during high water events. This type of habitat is denoted as "tapped basins" by Jorgenson and Brown (2005) in their characterization of Beaufort Sea coastlines, and is found only near Tangent Point and at Pitt Point/Pogik Bay (see below). Given that we observed large concentrations of staging shorebirds at both Tangent Point and Pitt Point/Pogik Bay, further investigation of the importance of this habitat for staging shorebirds may be warranted.

2.6.1.5. Smith Bay to Cape Halkett

The Smith Bay to Cape Halkett sub-region had a peak density during the fourth survey in 2006 of 14.9 birds/km. Although they did not systematically survey the area,

Connors et al. (1981) hypothesized that Pitt Point in this sub-region might attract large concentrations of postbreeding shorebirds due to the presence of extensive littoral flats and lagoon/slough edge habitat (also circled in Fig. 2.2b). We recorded large per-interval counts in both 2005 and the latter two surveys in 2006 at Pitt Point and nearby Pogik Bay, where the habitat is also classified as "tapped basins" by Jorgenson and Brown (2005; see above).

2.6.1.6. Colville Delta

We did not find the Colville Delta to be a shorebird concentration area as defined in this study, although Andres (1989) indicated this area was important to postbreeding dunlin and estimated that approximately 41 000 shorebirds of multiple species may pass through during fall staging. The visual homogeneity of the delta substrate (the area provides the most extensive salt marsh and mudflat habitat along the central Beaufort coast; Andres 1989) and how well it matches the plumage of a shorebird may have made it more difficult to locate shorebirds during aerial surveys, since it is the contrast of birds flying against background vegetation and water that enables their detection from the air. Relatively high numbers of semipalmated sandpipers and dunlin were recorded during the ground transect surveys at the Colville Delta camp in 2006, lending support to the idea that our aerial surveys may have failed to detect birds that were really present. Alternatively, if shorebirds move through the Colville delta in distinct pulses, our aerial surveys may have missed large groups of birds staging in the area. Andres (1994)

reported a sudden pulse of dunlin and sanderlings on shoreline silt barrens of the Colville delta in mid-August 1988 after high water receded.

2.6.1.7. Simpson Lagoon

This large lagoon system (in the Oliktok Point sub-region) did not contain large numbers of shorebirds during our aerial surveys in either year, and linear densities were 0-2 birds/km in 2006. In contrast, Johnson and Richardson (1981) observed 30-130 birds/km (mostly juvenile phalaropes, which numbered in the thousands) during the period 16-24 August 1977 and 1978. It is possible that we may have missed a similar pulse of phalaropes in Simpson Lagoon since we conducted no aerial surveys in the period 16-22 August 2005 or 2006, although Johnson and Richardson (1981) still observed relatively high densities during 23 August-1 September 1977 and 1978, when we conducted our last fixed-wing survey in 2006.

2.6.1.8. River deltas

Our data are equivocal with respect to describing the relative importance of river deltas for staging shorebirds. Because survey 2 in 2006 was the only one in which we surveyed all the Beaufort Coast deltas at once, we used high overall counts during this survey as the criteria for labeling a delta as a concentration area. For this reason, we named as concentration areas only the Sagavanirktok and Kongakut deltas, on which we observed 989 and 1024 birds, respectively, during survey 2 in 2006. Spindler (1979) recorded higher densities of shorebirds in the eastern lagoons of the Arctic Refuge than in the western lagoons, similar to our results from 2006. However, the eastern portion of

the Canning delta did support a relatively high per-interval density of shorebirds compared to other deltas during survey 3 in 2006, and had higher per-interval density of shorebirds relative to other deltas during just the Arctic Refuge survey in 2007. Martin and Moiteret (1981) reported peak linear densities of approximately 20 phalaropes/km during ground-based shoreline transects conducted on the Canning delta in 1980; we estimated 25.0 shorebirds/km (of all species) on the delta during survey 3 in 2006. Similarly, the Ikpikpuk delta had high total numbers of birds during the third and fourth surveys in 2006. Thus the importance of a given delta to staging shorebirds may vary within and across years, leading to the necessity of repeat surveys within a year and over long time periods to fully assess concentration areas.

2.6.1.9. Deltas versus coastlines

Spindler (1979) observed clusters of high bird density (mostly phalaropes, pectoral sandpipers, loons, and diving ducks) on the Canning, Okpilak-Hulahula, Jago, and Aichilik deltas during aerial surveys conducted 0.5 km inland of the Arctic Refuge coast in 1978 and 1979, indicating that at times, delta habitats may attract more birds than surrounding coastal areas. Andres (1989) found the Colville delta to be important to many species of postbreeding shorebirds, particularly dunlin. However, our data did not suggest that staging shorebirds used deltas at the exclusion of coastal areas. Shorebirds may move through staging areas in waves, using different littoral habitats within a region concurrently rather than cueing on specific coastal landforms. Also, use of coastal vs. delta areas likely varies by species due to differences in habitat present, and by wind and

weather conditions that create spatial and temporal differences in thermal cover and food availability (Connors and Risebrough, 1978; Martin and Moiteret, 1981).

2.6.1.10. Variability and reliability of aerial surveys for shorebirds

We observed a high level of spatial and temporal variability in the number and location of shorebirds staging on the ACP coast in 2005-2006, similar to other aerial surveys conducted across the ACP (Spindler, 1979; Gill et al., 1985; Johnson et al., 1993). Such variability is likely a result of both sampling error (i.e., failure to count birds that were actually present, which could occur for a variety of reasons: birds flying under the aircraft, birds not flushing in response to the aircraft, or errors in counting flock size) and inherent variability in shorebird numbers caused by underlying processes creating distribution and abundance patterns. Process variation includes changes in shorebird numbers between our survey dates due to migration timing, shoreline exposure, and food availability. High water events on Alaska's Arctic coast are primarily driven by wind patterns (which create storm surges) rather than by lunar tides. Thus water levels, and resulting shoreline/mudflat exposure and food availability, are temporally unpredictable. Skagen and Knopf (1993) concluded that variability in the exposure of ephemeral wetland complexes in the prairie pothole region of the Northern Great Plains significantly affected the distribution of migrating small shorebirds. In northern Alaska, Connors and Risebrough (1978) reported a correlation between wind direction and phalarope use of the leeward vs. windward shores of barrier islands in some years. Martin and Moiteret (1981) hypothesized that strong (and unpredictable) west wind events on the Canning

delta left deposits of benthic prey items on barrier island shores which then attracted large numbers of phalaropes for short periods of time. These results suggest that while aerial surveys may work well to discern large-scale patterns of shorebird distribution, population estimates based on such surveys could be biased if shorebird abundance changes rapidly in response to short-term variability in weather conditions, shoreline exposure, and food availability.

It is not appropriate to quantitatively compare our aerial and ground surveys because the ground transects were not located randomly within the study area. However, as a qualitative example of aerial survey validity we compared linear densities estimated from the aerial and ground surveys at Pt. Barrow/Elson Lagoon in 2006. To obtain an overall linear density for the ground surveys we totaled the number of individuals of all species seen in each survey period (1-16; see Methods) and divided by the total length of transects surveyed (9 km in each survey period). We compared these values to the linear densities for the four 2006 aerial surveys of the Pt. Barrow/Elson Lagoon sub-region (calculated by dividing the per-interval shorebird counts by 3.5 km as mentioned above). The aerial surveys recorded much lower densities than the ground surveys (Fig. 2.6), likely because the ground transects were located in known shorebird foraging areas, where higher densities would be expected than at random coastal locations. While the highest density recorded from the aerial surveys did coincide with higher densities observed on the ground transects, it is clear the peak of staging shorebird abundance in

the Barrow vicinity occurred between two of our aerial surveys and thus was not captured by this survey method.

We acknowledge these and other limitations of aerial surveys to detect true staging shorebird abundance and distribution, but we lack other adequate methods for monitoring a large number of small, mobile birds that cannot be detected remotely via satellite or GPS tracking devices. Development of such methods should be a priority, particularly for management of wildlife resources across large, remote areas like Alaska's northern coast. In the future, more frequent aerial surveys may help avoid missing occasions when shorebirds peak at a given site. Repeating aerial surveys over many years using the same methods would also provide more information on the degree of variability in shorebird numbers over time, which is necessary to detect trends in staging site use resulting from natural or anthropogenic causes. Unfortunately, we suspect that in many cases, financial costs and logistics (e.g., weather) may inhibit repetition of survey effort over many years.

2.6.2. Shorebird community characteristics from ground camps

2.6.2.1. Species richness, evenness, and diversity

We found that diversity (a combination of species richness and evenness) was lower on the Chukchi coast than on the Beaufort coast. This difference was likely due to species evenness on the Chukchi coast being lowered by the predominance of phalaropes, which in 2005 comprised 84% and 77% of shorebird sightings at the Peard Bay and Pt.

Barrow/Elson Lagoon camps, respectively, and 87% and 97% in 2006. In comparison, phalaropes comprised an average of 23% of all sightings at the three Beaufort Sea camps in 2005 and 2006. Species richness did not differ substantially between coasts in either year, although we expected it to be higher on the Chukchi coast if staging shorebird distribution reflects breeding distribution patterns (see species composition below; Johnson et al., 2007). This pattern of diversity is the reverse of that found when all staging birds (loons, waterfowl, shorebirds, and larids) were considered: species diversity was lower on the Beaufort coast due to dominance of the bird community by long-tailed ducks (*Clangula hyemalis*; Johnson et al., 1993).

2.6.2.2. Species composition

We expected the patterns of species composition at our ground camps to reflect how these same species are distributed during the breeding season (Connors, 1984). However, the patterns of distribution revealed in our study differed somewhat from that expectation, particularly later in the staging period. Two mechanisms may be responsible for this difference, likely acting in concert: 1) fall migration routes, and 2) habitat preference. Johnson et al. (2007) surmised that species-specific differences in breeding distribution of shorebirds were related to their spring migration routes. Distribution of postbreeding shorebirds, particularly later in the staging period, may likewise be related to fall migration routes. For example, dunlin are more common as breeders in the central portion of the ACP (Johnson et al., 2007), yet we also observed them in large numbers at Kasegaluk Lagoon on the Chukchi coast. The northern Alaska subspecies of dunlin

(*arcticola*) migrates to Asia for the winter (Warnock and Gill, 1996), so individuals likely leave breeding territories in the central ACP and migrate westward and southward along the Beaufort and Chukchi coasts, respectively, toward western Alaska and Asia. Less certain yet possibly still related to fall migration routes is the postbreeding distribution of red and red-necked phalaropes. Both species breed across the Arctic Coastal Plain, although red phalaropes are more common in the west while red-necked phalaropes seem to favor inland wet-tundra breeding sites over coastal areas (Johnson and Herter, 1989; Johnson et al., 2007). We rarely observed red phalaropes on the coast at our two eastern-most ground camps (Sagavanirktok and Okpilak), which may indicate a movement of this species toward the western Beaufort and Chukchi coasts from which they migrate pelagically south through the Bering Sea (although Johnson and Richardson (1981) recorded an average of 4:1 red to red-necked phalaropes in Simpson Lagoon to the east of the Colville river delta). Red-necked phalaropes were found in much larger numbers at our eastern ground camps, despite their ACP-wide breeding distribution. It is unknown which direction Alaska-breeding red-necked phalaropes take on fall migration, but one speculation is they may fly eastward to join northern Canada-breeding populations that stage in the Bay of Fundy in early fall (Rubega et al., 2000). The eastern-trending distribution of red-necked phalaropes along the ACP coast during the staging period may lend support to this idea.

The postbreeding distribution patterns we observed may also be related to preferred staging habitat. Johnson et al. (2007) reported pectoral sandpipers, long-billed

dowitchers, and American golden-plovers as common breeding species across the entire ACP. However, none of these species were abundant at coastal staging areas, likely due to their propensity to stage in non-littoral tundra habitats (Connors et al., 1981; A. Taylor, *pers. obs.*).

Our ground-based surveys also provided an opportunity to compare our data on relative abundance of various shorebird species with that collected by previous researchers. We found notable differences in relative abundance of dunlin and western sandpipers between this study and previous work done on the northern Alaska coast. Lehnhausen and Quinlan (1981) reported seeing flocks of >1,000 dunlin using Kasegaluk Lagoon during mid-August 1980. Although we did not survey the entirety of Kasegaluk Lagoon in 2006, the largest flocks observed by our ground crew were of 100-200 individuals. Connors et al. (1981) observed 2110 dunlin over four years at Barrow during transect surveys that totaled approximately 200 km, while we recorded a total of only 647 dunlin at Barrow over two years during transect surveys that totaled 252 km. We did record large numbers of staging dunlin at the Colville delta, similar to Andres' (1989) study. These apparent declines in dunlin numbers at several staging sites mirrors a 50% decline in breeding density at Prudhoe Bay documented between 1981 and 1992 (Troy Ecological Research Associates, 1993). It is still unclear, however, whether the differences in staging site numbers are related to large interannual variability in shorebird population sizes that result from differential use of staging sites across years or from variable breeding productivity in a given year (Gill et al., 1985).

When comparing species composition at ACP staging areas, Andres (1989) found that western sandpipers were relatively more abundant at the Colville delta than at Pt. Barrow, comprising 4% (his data) and 2% (Connors, 1984) of all shorebird observations, respectively. However, we found western sandpipers were more numerous at all Chukchi coast camps (Kasegaluk Lagoon, Peard Bay, and Pt. Barrow/Elson Lagoon) than at the Colville Delta camp in 2005 and 2006. This species has long been assumed to be a rare breeder on the ACP, occurring mostly on the Yukon-Kuskokwim Delta more than 500 km to the south (Johnson and Herter, 1989; Wilson, 1994). However, recent studies have shown that western sandpipers may have a larger breeding range on the ACP than previously thought, nesting in low densities across the entire western half of the region (Cotter and Andres, 2000; Johnson et al., 2007). Whether this is a recent change as a result of a warming Arctic climate, or because early studies of breeding shorebirds on the ACP were limited in scope and length is unknown. It is possible that some of the postbreeding western sandpipers observed on the Chukchi coast may be from a population that breeds on the Chukotski Peninsula in Russia (Kozlova, 1962). Additional research using genetic data and/or individuals marked on the breeding grounds in the U.S. and Russia could help answer this question.

2.6.2.3. Phenology

Accelerated rates of warming in the Arctic (Sereze and Francis, 2006) may have a large impact on the phenology of shorebird staging on the northern Alaska coast. Advancement of spring phenology is a highly apparent result of global warming thus far

(Durant et al., 2007); the average snowmelt date in northern Alaska has advanced ~8 days since the 1960's (Stone et al., 2002). If accelerated snowmelt in the Arctic results in earlier shorebird breeding phenology, fledging of chicks and movement of shorebirds to coastal areas may begin earlier. On the other hand, there is some evidence to suggest that Arctic-breeding shorebirds are capable of replacing clutches lost early in incubation (Naves et al., 2008). If a warming Arctic climate results in a longer period of favorable weather (Callaghan et al., 2005), movements of birds to coastal staging areas could be delayed if more individuals replace lost clutches (or attempt second clutches) and chicks fledge later in the breeding season (Jenni and Kery, 2003). These two effects may also act in concert, in which case the timing of peak staging should remain the same. However, the overall length of the staging period should then increase due to less synchrony in chick fledging and subsequent arrival of adults and juveniles at staging areas.

Several observed differences between data collected at our ground camps and previous research on the phenology of staging on the northern Alaska coast suggest shorebirds may be staging earlier now than in previous decades. Lehnhausen and Quinlan (1981) reported a peak in dunlin use of beach transects at Kasegaluk Lagoon in mid-August 1980, whereas in our study the peak was approximately two weeks earlier. Similarly, Gill et al. (1985) reported a peak in red phalarope abundance at Peard Bay in mid-August in 1983, whereas our data show a peak in early August. Johnson (1978) and Johnson and Richardson (1981) recorded the highest densities of staging phalaropes at

Simpson Lagoon between 10-20 August 1977 and 19-24 August 1978, respectively, whereas we observed the highest counts of phalaropes between 1-9 August at the Sagavanirktok camp (close to Simpson Lagoon) in 2005 and 2006. However, we cannot be sure whether these differences reflect annual variation in how and when shorebirds use the coast or true changes in phenology over time.

While dunlin and phalarope staging phenology may be advancing, western sandpiper phenology may be delayed relative to that previously reported. Johnson et al. (1993) reported that western sandpipers were the most common small shorebird along Kasegaluk Lagoon shorelines in late July and early August 1990-1991, after which their numbers declined. In our study, western sandpipers did not become more numerous than dunlin or semipalmated sandpipers at Kasegaluk Lagoon until mid-August in 2006, possibly indicating a delay in the movement of western sandpiper juveniles from tundra breeding areas to coastal staging areas, or from other breeding populations to northern Alaska (see above). This is similar to a pattern described by Jenni and Kery (2003), wherein peak fall passage times for short-distance migrant songbirds in Switzerland have been delayed 3.4 days over four decades. Of all common species staging on the northern Alaska coast, western sandpipers have the shortest total migration length (Wilson, 1994), so they may be more likely to delay staging and migration than other species with longer migration distances. Alternatively, this pattern may reflect the fact that 2006 was a relatively late year for spring phenology (six days later than the five-year average for

snow melt date measured at Barrow) and thus may have resulted in delayed onset of shorebird breeding and subsequent staging behavior.

2.6.2.4. Habitat selection

Habitat selection by postbreeding shorebirds in this study was similar to the patterns of habitat use reported by Connors et al. (1981) from their studies at Pt. Barrow in 1975-1979. Like us, they found evidence for several distinct foraging guilds (gravel beach, mudflat, and salt marsh/pond edge), and species composition of these guilds was comparable to ours. We interpret this to mean that species-habitat associations for shorebirds staging along the northern Alaska coastline are relatively invariant through time. Anecdotal observations indicate that localized habitat availability and therefore selection by postbreeding shorebirds were likely affected by wind or weather patterns. Data that inform predictions of how wind speed/direction and rainfall affect water levels at coastal staging sites on the ACP would be particularly useful in understanding the mechanisms underlying variation in shorebird distribution and habitat selection, and in predicting how climate-related changes in weather patterns may affect habitat availability for staging shorebirds. For example, there were fewer dunlin and semipalmated sandpipers at Pea Island (North Carolina) and Merritt Island (Florida) National Wildlife Refuges as water depth increased, but dunlin preferred deeper water than semipalmated sandpipers at local scales (Collazo et al., 2002). In addition to knowledge of the amount of terrestrial habitat exposed, predictions of water levels along shorelines and in coastal ponds and lagoons are important because shorebird species staging on the ACP coast

differ generally in size, and particularly in tarsus and bill length (both morphological characteristics that determine the depth of water in which the species is able to feed). Thus variation in water levels may affect habitat selection and species composition at a particular location.

2.6.3. Conservation implications

Our data indicate that some littoral areas on the ACP attracted large numbers of shorebirds during our study (concentration areas) while other seemingly suitable areas were not as heavily used. Disturbance from industrial or anthropogenic development would have a larger impact on shorebirds at heavily used sites than at sites of lesser importance, although synergistic effects of disturbance and climate change are difficult to predict. Additionally, given existing infrastructure and the probable development of new oil and gas fields along the northern Alaska coast (Bird et al., 2008), the potential exists for a significant oil spill to occur somewhere in the ACP littoral zone during the ice-free season, when shorebirds are present. Such an event could affect a substantial segment of a shorebird species or population if it affects a postbreeding concentration area and results in oiling of birds' plumage or food supply. Juvenile shorebirds may be particularly susceptible to oiling: juvenile red and red-necked phalaropes did not at first differentiate between oiled and non-oiled surface water during trials conducted at Pt. Barrow (Connors et al., 1981). Habitat suitability could also be reduced through oiling of coastlines, which may reduce forage quality and availability. The impact of an oil spill

could be extensive: because river/ocean currents and wind-driven waves move the oil along the coast, staging areas many kilometers from development sites may be affected.

Increasing industrial activity will also likely increase the human footprint in the Arctic, which could affect patterns of species prevalence, distribution, and habitat use in unpredictable ways if artificial habitats, such as roads, pipelines, gravel pads, or treatment ponds, become more common. For example, over the course of the staging period in 2006, we counted 5512 phalaropes (almost half of the total observed on ground transects during 2006) in the Barrow sewage treatment lagoon. These individuals were not included in our analyses because they were not located on our survey transects, and there was no comparable habitat type at the other staging sites we studied. Should artificial habitats become common enough, some species may stage there preferentially, leading to changes in abundance of staging shorebirds in natural coastal habitats. This type of change would be important to consider when examining trends in postbreeding shorebird distribution and abundance through time.

Lastly, phenology is a very apparent mechanism through which effects of climate change on Arctic bird populations may be observed (Walther et al., 2002). We documented that dunlin and red phalaropes may have advanced their staging phenology in recent decades as a result of changing environmental conditions. Conversely, western sandpipers may be delaying their staging phenology. These data provide a baseline for developing testable hypotheses regarding the effects of climate change on the length and timing of the staging period on the ACP coast. An understanding of how the initiation

and termination of breeding and staging periods may change in response to changing climatic conditions is essential for developing monitoring protocols which account for variation in when individuals are most visible or available for observation. Repeating studies such as ours to document phenological changes resulting from changing environmental conditions will be important for long-term monitoring.

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2.8 Literature cited

ACIA. 2005. Impacts of a warming Arctic: Arctic climate impact assessment. 1042 pp. Cambridge, UK: Cambridge University Press. http://www.acia.uaf.edu.

Alldredge, J.R., and Griswold, J. 2006. Design and analysis of resource selection studies for categorical resource variables. Journal of Wildlife Management 70:337-346.

Andres, B.A. 1989. Littoral zone use by post-breeding shorebirds on the Colville River Delta, Alaska. M.S. Thesis, Ohio State University, Columbus, OH.

Andres, B.A. 1994. Coastal zone use by postbreeding shorebirds in northern Alaska. Journal of Wildlife Management 58:206-213.

Bird, K.J., Charpentier, R.R., Gautier, D. L., Houseknecht, D.W., Klett, T.R., Pittman, J.K., Morre, T.W., Schenk, C.J., Tennyson, M.W., and Wandrey, C.J. 2008. Circum-arctic resource appraisal: estimates of undiscovered oil and gas north of the Arctic Circle. USGS Fact Sheet 2008-3049. http://pubs.usgs.gov/fs/2008/3049/

Brown, S., Hickey, C., Harrington, B., and Gill, R., eds. 2001. United States Shorebird Conservation Plan, 2nd ed. Manomet, Massachusetts: Manomet Center for Conservation Sciences. http://www.fws.gov/shorebirdplan/USShorebird/PlanDocuments.htm.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L., and Thomas, L. 2001. Introduction to distance sampling: estimating abundance of biological populations. New York: Oxford University Press.

Burger, J. 1981. The effect of human activity on birds at a coastal bay. Biological Conservation 21:231-241.

Burger, J., Carlucci, S. A., Jeitner, C. W., and Niles, L. 2007. Habitat choice, disturbance, and management of foraging shorebirds and gulls at a migratory stopover. Journal of Coastal Research 23:1159-1166.

Callaghan, T., Björn, L.O., Chapin III, F.S., Chernov, Y., Christensen, T.R., Huntley, B., Ims, R., et al. 2005. Arctic tundra and polar desert ecosystems. Arctic Climate Impact Assessment. Cambridge: Cambridge University Press. 243-352.

Collazo, J.A., O'Hara, D.A., and Kelly, C.A. 2002. Accessible habitat for shorebirds: factors influencing its availability and conservation implications. Waterbirds 25 (Special Publication 2):13-24.

Connors, P.G. 1984. Ecology of shorebirds in the Alaskan Beaufort littoral zone. In: Barnes, R., Shell, D.M., and Ramirez, E., eds. The Alaskan Beaufort Sea: Ecosystems and environments. New York: Academic Press. 403– 416.

Connors, P.G., and Risebrough, R.W. 1978. Shorebird dependence on arctic littoral habitats. Annual Report, RU-0172, Outer Continental Shelf Environment Assessment Program. Boulder, CO: Bureau of Land Management/National Oceanic and Atmospheric Administration. Available at the Alaska Resources Library and Information Services. http://www.arlis.org.

Connors, P.G., Connors, C.S., and Smith, K.G. 1981. Shorebird littoral zone ecology of the Alaska Beaufort Coast. Anchorage: Bureau of Land Management/National Oceanic and Atmospheric Administration, Outer Continental Shelf Environmental Assessment Program. Final Reports of Principal Investigators 23:295– 396. Available at the Alaska Resources Library and Information Services. http://www.arlis.org.

Connors, P.G., Myers, J.P., and Pitelka, F.A. 1979. Seasonal habitat use by Arctic Alaskan shorebirds. Studies in Avian Biology 2:101–111.

Cotter, P.A., and Andres, B.A. 2000. Nest density of shorebirds inland from the Beaufort Sea Coast, Alaska. Canadian Field-Naturalist 114:287-291.

Craig, E. H., Craig, T. H., Huettmann, F., and Fuller, M.R. 2009. Use of machine learning algorithms to predict the incidence of lead exposure in Golden Eagles. In: Watson, R.T., Fuller, M., Pokras, M., and Hunt, W.G., eds. Ingestion of lead from spent ammunition: implications for wildlife and humans. The Peregrine Fund, Boise, Idaho, USA. DOI 10.4080/ilsa.2009.0303.

Durant, J.M., Hjermann, D.O., Ottersen, G., and Stenseth, N.C. 2007. Climate and the match or mismatch between predator requirements and resource availability. Climate Research 33:271-283.

ESRI, Inc. 2005. ESRI®ArcGIS™ 9.1, Redlands, California.

Friedman, J. 2001. Greedy function approximations: a gradient boosting machine. Annals of Statistics 29:1189–1232.

Gilders, M.A., and Cronin, M.A. 2000. North Slope oil field development. In: Truett, J.C., and Johnson, S.R., eds. The natural history of an Arctic oil field. San Diego: Academic Press. 15–33.

Gill, R.E., Handel, C.H., and Connors, P.C. 1985. Bird utilization of Peard Bay and vicinity. In: Kinney, P.J., ed. Environmental characterization and biological utilization of Peard Bay. Anchorage: Bureau of Land Management/National Oceanic and Atmospheric Administration, Outer Continental Shelf Environmental Assessment Program. Final Reports of Principal Investigators 35:244-323. Available at the Alaska Resources Library and Information Services. http://www.arlis.org.

Hinzman, L..D., Bettez, N.D., Bolton, W.R., Chapin, F.S., Dyurgerov, M.B., Fastie, C.L., Griffith, B., et al. 2005. Evidence and implications of recent climate change in northern Alaska and other arctic regions. Climate Change 72:251-298.

Hochachka, W.M., Caruana, R., Fink, D., Munson, A., Riedewald, M., Sorokina, D., and Kelling, S. 2007. Data-mining discovery of pattern and process in ecological systems. Journal of Wildlife Management 71:2427-2437.

Holland, M.M., and Bitz, C.M. 2003. Polar amplification of climate change in coupled models. Climate Dynamics 21:221–232.

Holmgren, N., Ellegrin, H., and Pettersson, J. 1993. Stopover length, body mass, and fuel deposition rate in autumn migrating dunlins *Calidris alpina*: evaluating the effects of moulting status and age. Ardea 81:9-19.

International Wader Study Group. 2003. Waders are declining worldwide: conclusions from the 2003 International Wader Study Group Conference, Cadiz, Spain. Wader Study Group Bulletin 101/102:8-12.

IPCC. 2001. Climate change 2001: The scientific basis. Contribution of Working Group I to the third assessment report of the Intergovernmental Panel on Climate Change. Cambridge: Cambridge University Press. Available from Cambridge University Press, The Edinburgh Building, Shaftesbury Road, Cambridge CB2 2RU England

Jenni, L., and Kery, M. 2003. Timing of autumn bird migration under climate change: advances in long-distance migrants, delays in short-distance migrants. Proceedings of the Royal Society of London. B 270:1467–1471; DOI 10.1098/rspb.2003.2394.

Johnson, J.A., Lanctot, R.B., Andres, B.A., Bart, J.R., Brown, S.C., Kendall, S.J., and Payer, D.C. 2007. Distribution of breeding shorebirds on the Arctic Coastal Plain of Alaska. Arctic 60:277-293.

Johnson, S.R. 1978. Beaufort Sea Barrier Island-Lagoon ecological process studies, section II: avian ecology in Simpson Lagoon, 1977. Boulder, CO: Bureau of Land Management/National Oceanic and Atmospheric Administration, Outer Continental Shelf Environmental Assessment Program. Available at the Alaska Resources Library and Information Services. http://www.arlis.org.

Johnson, S.R., and Herter, D.R. 1989. The birds of the Beaufort Sea. Anchorage: British Petroleum Exploration (Alaska), Inc.

Johnson S.R., and Richardson, W.J. 1981. Beaufort Sea Barrier Island-Lagoon ecological process studies, Part 3: Birds. Environmental Assessment of the Alaskan Continental Shelf, Final Reports of Principal Investigators Vol. 7: Biological studies. Prepared for National Oceanic and Atmospheric Administration/Bureau of Land Management. Available at the Alaska Resources Library and Information Services. http://www.arlis.org.

Johnson, S.R., Wiggins, D.A., and Wainwright, P.F. 1993. Late-summer abundance and distribution of marine birds in Kasegaluk Lagoon, Chukchi Sea, Alaska. Arctic 46:212-1227.

Jorgenson, M.T., and Brown, J. 2005. Classification of the Alaskan Beaufort Sea coast and estimation of carbon and sediment inputs from coastal erosion. Geo-Marine Letters 25:69-80.

Kowalewski, M., Kiessling, W., Aberhan, M., Fursich, F.T., Scarponi, D., Barbour Wood, S.L., and Hoffmeister, A.P. 2006. Ecological, taxonomic, and taphonomic components of the post-Paleozoic increase in sample-level species diversity of marine benthos. Paleobiology 32:533-561.

Kozlova, E.V. 1962. [Fauna of U.S.S.R—Charadriiformes, Limicolae.] Leningrad: Leningrad-skoe Otdelenie.

Lehnhausen, W.A., and Quinlan, S.E. 1981. Bird migration and habitat use at Icy Cape, Alaska. Anchorage: U.S. Fish and Wildlife Service, unpublished report. Available at the Alaska Resources Library and Information Services. http://www.arlis.org.

Lyons, J.E. and Haig, S.M. 1995. Fat content and stopover ecology of spring migrant Semipalmated Sandpipers in South Carolina. Condor 97:427-437.

Manly, B.F.J., McDonald L.L., Thomas, D.L., McDonald, T.L. and Erickson, W.P. 2002. Resource selection by animals: statistical design and analysis for field studies, 2nd ed. Dordrecht, Netherlands: Kluwer Academic Publishers.

Martin, P.D., and Moiteret, C.S. 1981. Bird populations and habitat use, Canning River Delta, Alaska. Fairbanks: U.S. Fish and Wildlife Service. Available at the Alaska Resources Library and Information Services. http://www.arlis.org.

McCarty, J.P. 2001. Ecological consequences of recent climate change. Conservation Biology 15: 320-331.

Maclean, I.M.D., Austin, G.E., Rehfisch, M.M., Blew, J., Crowe, O., Delany, S., Devos, K., et al. 2008. Climate change causes rapid changes in the distribution and site abundance of birds in winter. Global Change Biology 14:2489-2500.

Meltofte, H., Hoye, T.T., and Scnmidt, N.M. 2008. Effects of food availability, snow, and predation on breeding performance of waders at Zackenberg. Advances in Ecological Research 40: 325-343.

National Research Council. 2003. Cumulative environmental effects of oil and gas activities on Alaska's North Slope. Washington, D.C.: National Academies Press.

Naves, L.C., Lanctot, R.B., Taylor, A.R. and Coutsoubos, N.P. 2008. How often do Arctic shorebirds lay replacement clutches? Wader Study Group Bulletin 115: 2–9.

Pielou, E.C. 1974. Population and community ecology: principles and methods. New York: Gordon and Breach Science Publishers, Inc.

Rubega, M.A., Schamel, D. and Tracy, D.M. 2000. Red-necked Phalarope (*Phalaropus lobatus*). In: A. Poole, ed. The Birds of North America Online. Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/538

Salford Systems, Inc. 2003. TreeNet Questions and Answers. http://www.salfordsystems.com/faq4TreeNet.php.

SAS Institute, Inc. 2003. SAS Version 9.1, Cary, NC, USA.

Sereze, M.C., and Francis. J.A. 2006. The polar amplification debate. Climate Change 76:241-264.

Sereze, M.C., Walsh, J.E., Chapin III, F.S., Osterkamp, T., Dyurgerov, M., Romanovsky, V., Oechel, W.C., Morison, J., Zhang, T., and Barry, R.G. 2000. Observational evidence of recent change in the northern high-latitude environment. Climatic Change 46:159-207.

Skagen, S.K., and Knopf, F.L. 1993. Toward conservation of midcontinental shorebird migrations. Conservation Biology 7:533-541.

Smit, C., and Visser, J.M. 1993. Effects of disturbance on shorebirds: a summary of existing knowledge from the Dutch Wadden Sea and Delta area. Wader Study Group Bulletin 68: 6–19.

Snedecor, G.W., and Cochran, W.G. 1980. Statistical methods, 7th ed. Ames, IA: Iowa State University Press.

Spindler, M.A. 1979. Bird populations in coastal habitats, Arctic National Wildlife Range, Alaska: results of 1978 and 1979 aerial surveys. Unpubl. ms. Available from U.S. Fish and Wildlife Service, Arctic National Wildife Refuge, 101 12th Avenue, Room 236,
Fairbanks, Alaska 99701.

Stein, B.A., and Davis, F.W. 2000. Discovering life in America: tolls and techniques of biodiversity inventory. In: Stein, B.A., Kutner, L.A., and Adams, J.A., eds. Precious heritage: the status of biodiversity in the United States. Oxford: The Nature Conservancy and Oxford University Press. 19-54.

Stone, R.S., Dutton, E.G., Harris, J.M., and Longenecker, D. 2002. Earlier spring snowmelt in northern Alaska as an indicator of climate change. Journal of Geophysical Research 107 (D10): pages 10-1 to 10-15.

Thomas, L., Laake, J.L., Strindberg, S., Marques, F.F.C., Buckland, S.T., Borchers, D.L., Anderson, D.R., et al. 2006. Distance 5.0. Release 2. Research Unit for Wildlife Population Assessment, University of St. Andrews, UK. http://www.ruwpa.st-and.ac.uk/distance/.

Troy Ecological Research Associates. 1993. Population dynamics of birds in the Pt. McIntyre reference area 1981–1992. Anchorage: BP Exploration (Alaska), Inc. Available at the Alaska Resources Library and Information Services. http://www.arlis.org.

Tulp, I., and Schekkerman, H. 2008. Has prey availability for Arctic birds advanced with climate change? Hindcasting the abundance of tundra arthropods using weather and seasonal variation. Arctic 61:48-60.

U.S. Shorebird Conservation Plan. 2004. High priority shorebirds – 2004. Unpubl. report. Available from U.S. Fish and Wildlife Service, 4401 N. Fairfax Dr., MBSP 4107, Arlington, VA, 22203 U.S.A. 5 pp.

Van Der Jeugd, H.P., Eichhorn, G., Litvin, K.E., Stahl, J., Larsson, K.L., Van Der Graaf, A.J., and Drent, R.H. 2009. Keeping up with early springs: rapid range expansion in an avian herbivore incurs a mismatch between reproductive timing and food supply. Global Change Biology 15:1057-1071.

Walther, G., Post, E., Convey, P., Menzal, A., Parmesank, C., Beebee, T.J.C., Fromentin, J., Heogh-Guldberg O., and Bairlein, F. 2002. Ecological responses to recent climate change. Nature 416:389-395.

Ward, D.H., Stehn, R.A., Erickson, W.P., and Derksen, D.V. 1999. Response of fall-staging brant and Canada geese to aircraft overflights in southwestern Alaska. Journal of Wildlife Management 63:373-381.

Warnock, N..D., and Gill, R.E. 1996. Dunlin (*Calidris alpina*). In: Poole, A., ed. The Birds of North America Online. Ithaca: Cornell Lab of Ornithology. Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/203; DOI:10.2173/bna.203.

Wilson, W. H. 1994. Western Sandpiper (*Calidris mauri*). In: Poole, A., ed. The Birds of North America Online. Ithaca: Cornell Lab of Ornithology. Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/090; DOI:10.2173/bna.90.

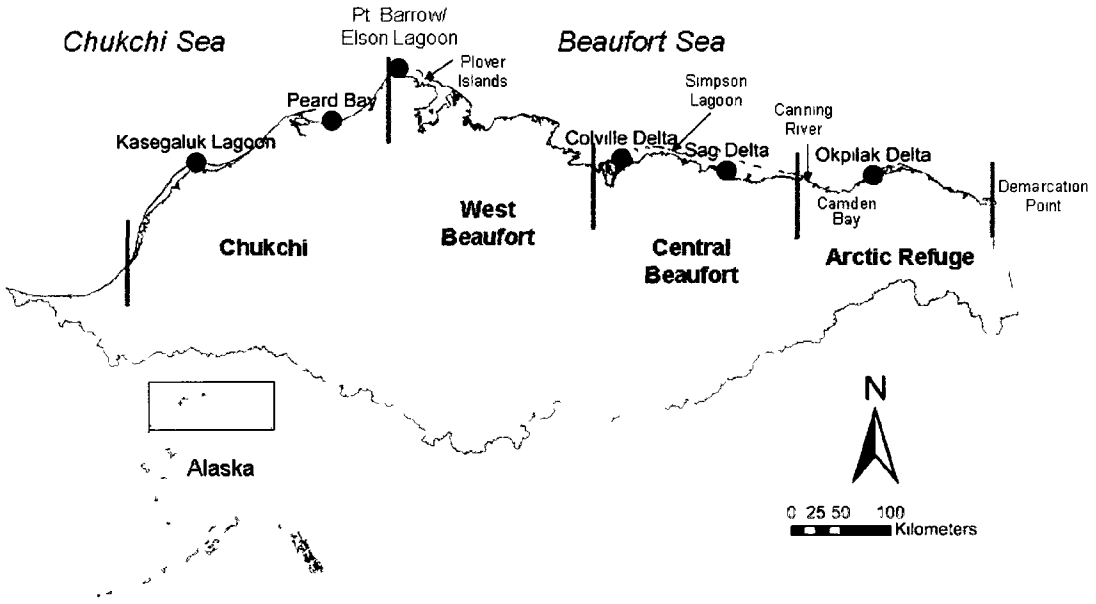
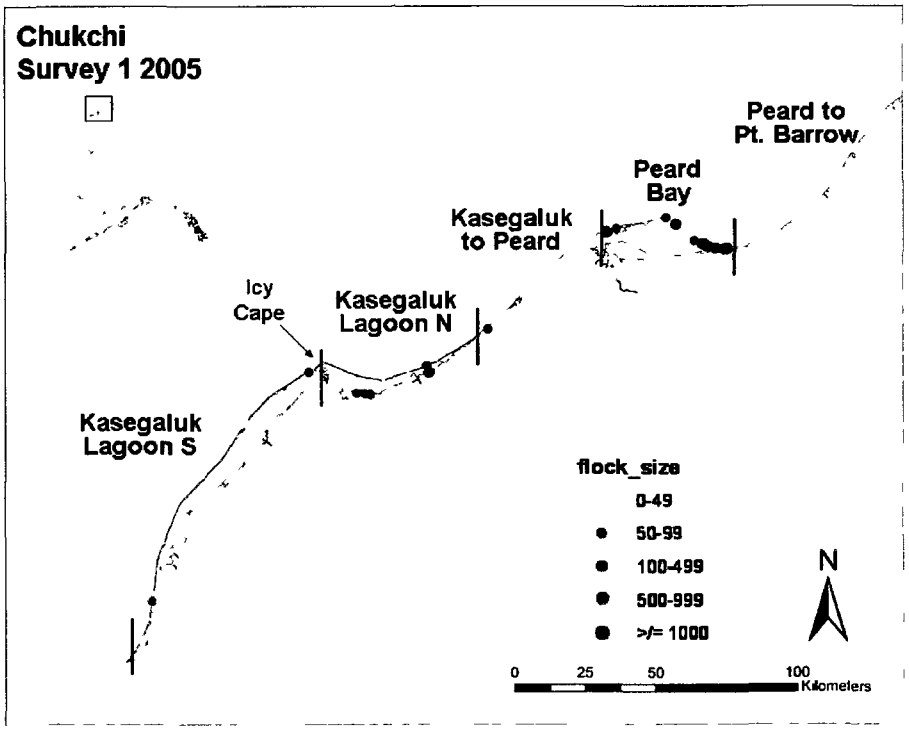
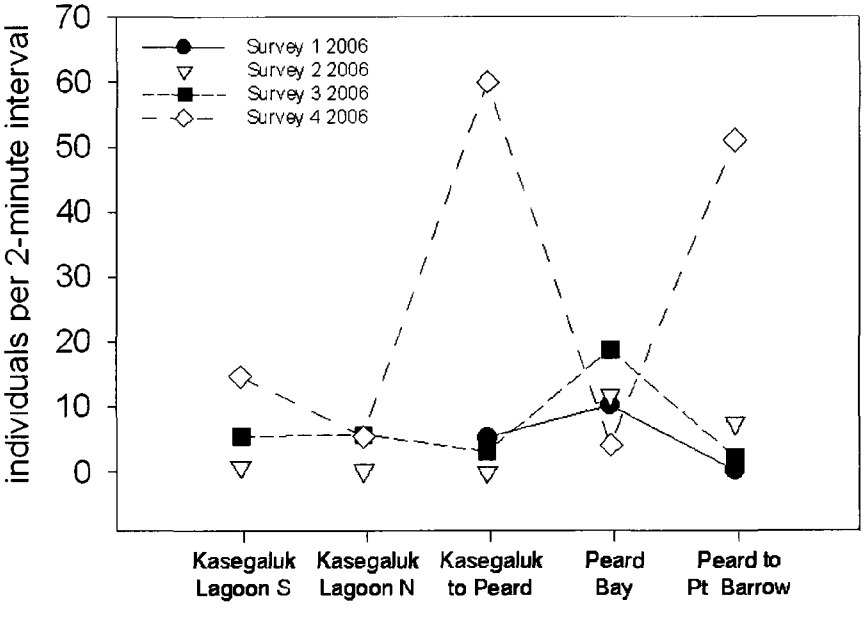
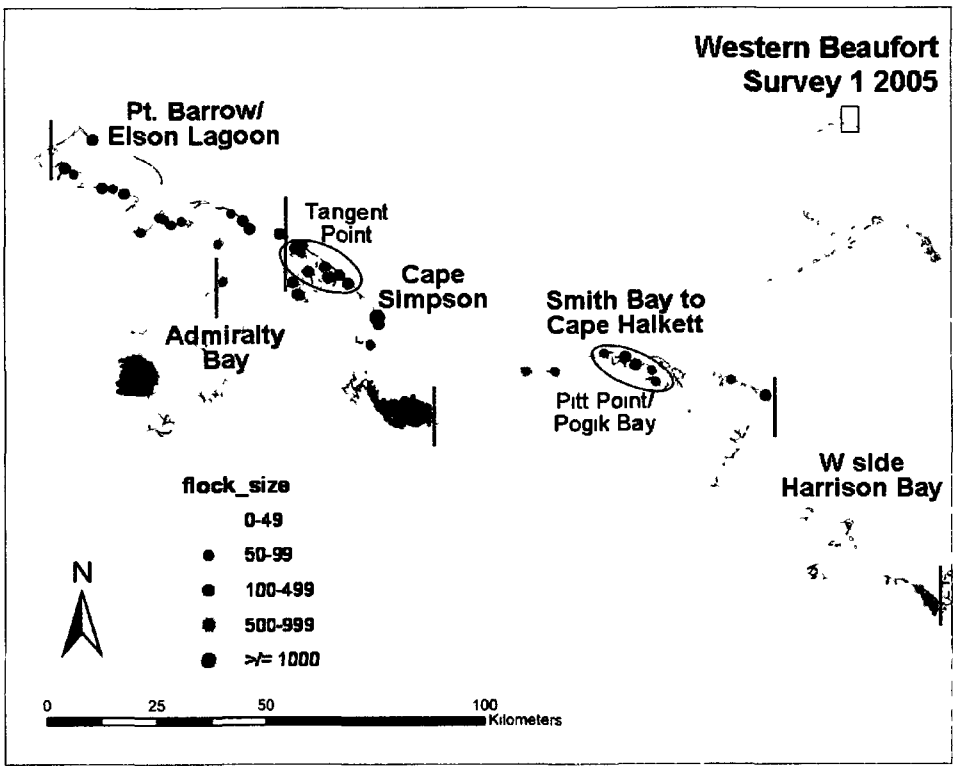
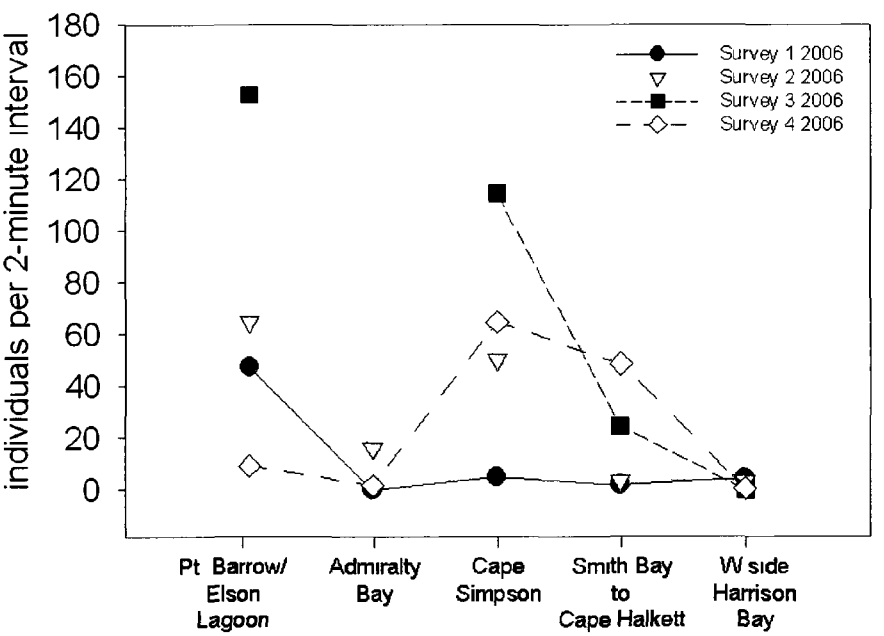


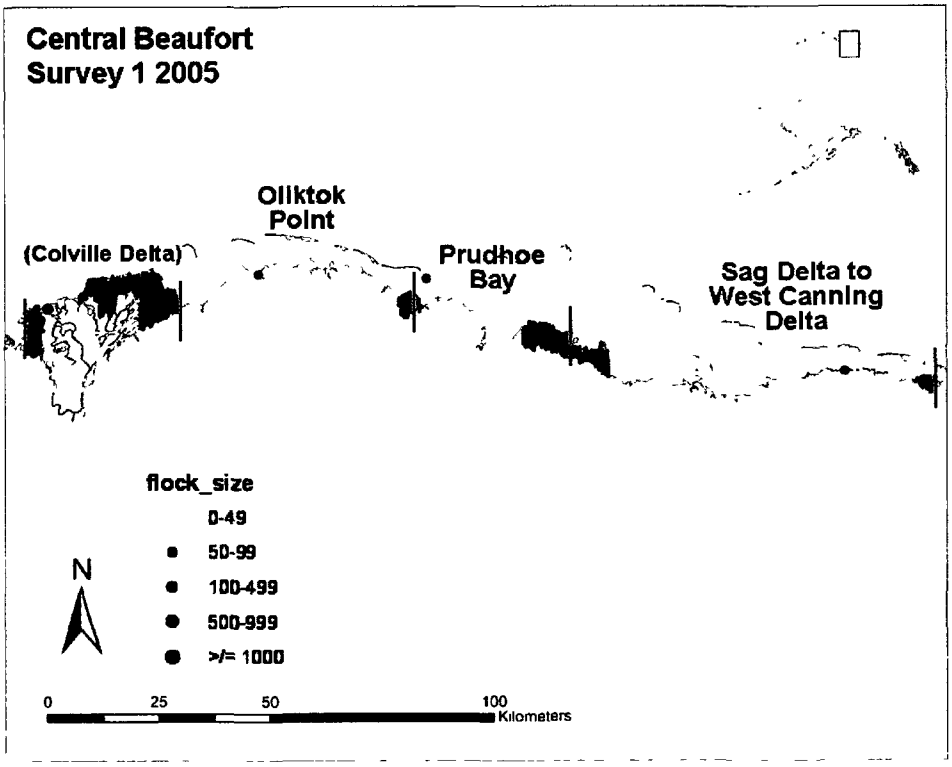
Figure 2.1. Aerial survey regions and ground camp locations, 2005-2007. Dark vertical lines indicate boundaries of regions; the west (southwest end of Kasegaluk Lagoon) and east (Demarcation Point) boundaries of the study area are the furthest west and east vertical lines, respectively. Sag = Sagavanirktok.

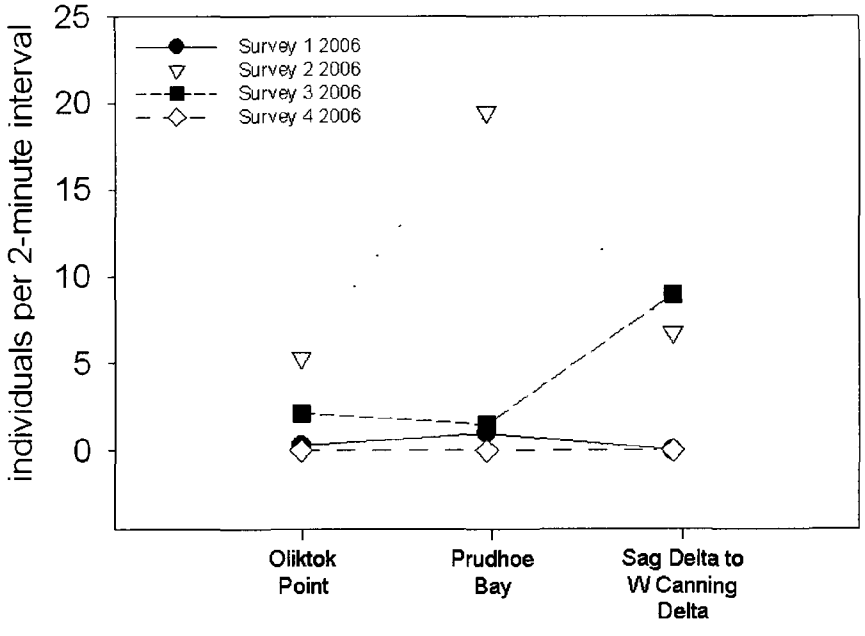

Chukchi
Survey 1 2005
Peard to
Pt. Barrow
Peard
Bay
Kasegaluk
to Peard
Icy
Cape
Kasegaluk
Lagoon N
Kasegaluk
Lagoon S
flock_size
0-49
50-99
100-499
500-999
>/= 1000
N
0
25
50
100
Kilometers

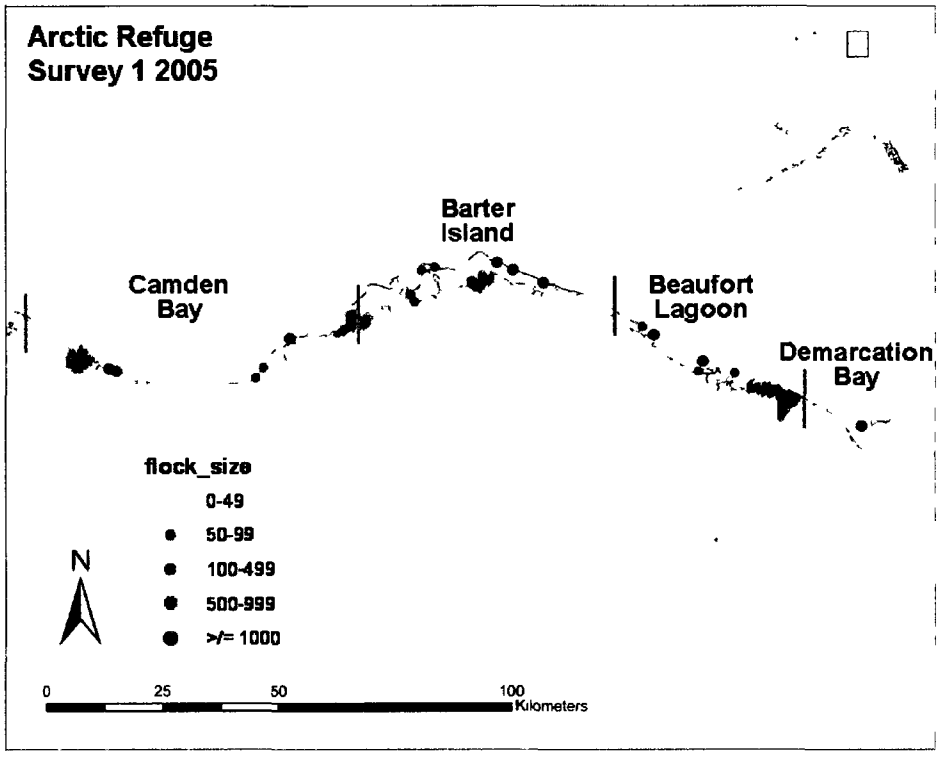

individuals per 2-minute interval
70
60
50
40
30
20
10
0
Survey 1 2006
Survey 2 2006
Survey 3 2006
Survey 4 2006
Kasegaluk
Lagoon S
Kasegaluk
Lagoon N
Kasegaluk
to Peard
Peard
Bay
Peard to
Pt Barrow


Western Beaufort
Survey 1 2005
Pt. Barrow/
Elson Lagoon
Tangent
Point
Cape
Simpson
Admiralty
Bay
Smith Bay to
Cape Halkett
Pitt Point/
Pogik Bay
W side
Harrison Bay
flock_size
0-49
50-99
100-499
500-999
>/= 1000
N
0
25
50
100
Kilometers


individuals per 2-minute interval
180
160
140
120
100
80
60
40
20
0
Survey 1 2006
Survey 2 2006
Survey 3 2006
Survey 4 2006
Pt Barrow/
Elson
Lagoon
Admiralty
Bay
Cape
Simpson
Smith Bay
to
Cape Halkett
W side
Harrison
Bay


Central Beaufort
Survey 1 2005
Oliktok
Point
(Colville Delta)
Prudhoe
Bay
Sag Delta to
West Canning
Delta
flock_size
0-49
50-99
100-499
500-999
>/= 1000
N
0
25
50
100
Kilometers


individuals per 2-minute interval
25
20
15
10
5
0
Survey 1 2006
Survey 2 2006
Survey 3 2006
Survey 4 2006
Oliktok
Point
Prudhoe
Bay
Sag Delta to
W Canning
Delta


Arctic Refuge
Survey 1 2005
Barter Island
Camden Bay
Beaufort Lagoon
Demarcation Bay
flock_size
0-49
50-99
100-499
500-999
>/= 1000
N
0
25
50
100
Kilometers

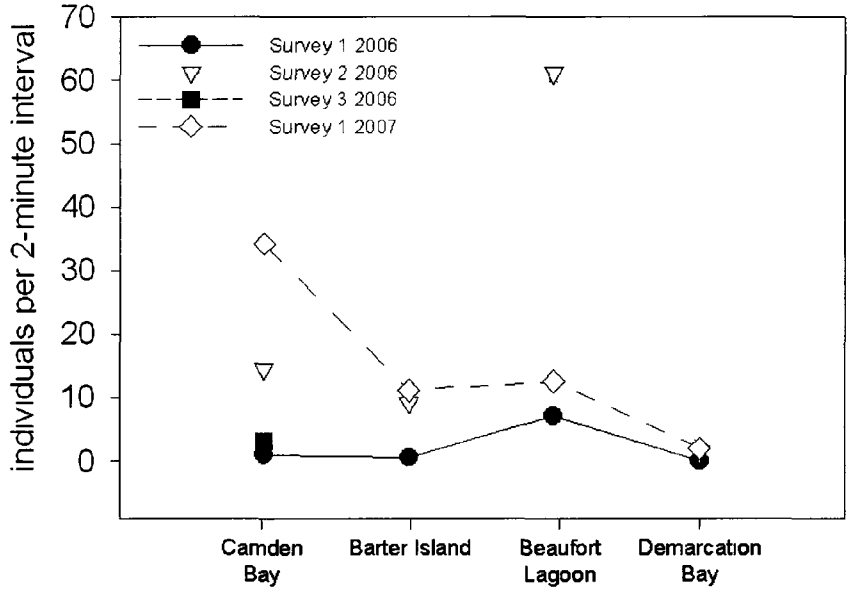

individuals per 2-minute interval
70
60
50
40
30
20
10
0
Survey 1 2006
Survey 2 2006
Survey 3 2006
Survey 1 2007
Camden Bay
Barter Island
Beaufort Lagoon
Demarcation Bay

Figure 2.2. Aerial distribution of shorebirds observed along the coast of northern Alaska, 2005-2007. Maps show aerial survey sub-region endpoints (vertical black lines) and shorebird abundance categorized per two-minute survey interval (colored dots) along the coast of northern Alaska, based on data from 2005 helicopter survey. Shorebird abundance categories are as follows: blue dot: 50-99 birds; red dot: 100-499 birds; green dot: 500-999 birds; purple dot: $\geq$ 1000 birds. No dot indicates there were fewer than 50 birds counted in that two-minute interval. Gray shaded areas represent river delta transects for which no 2005 data exist. Graphs below each map show results for the four 2006 and single 2007 fixed-wing surveys. Each symbol represents the mean per-interval count of shorebirds for each survey/sub-region combination. A lack of symbols on the graph for a given survey period indicates that no aerial surveys were conducted in that sub-region in that period. First panel = Chukchi region, second panel = western Beaufort region, third panel = Central Beaufort region, and fourth panel = Arctic Refuge region.

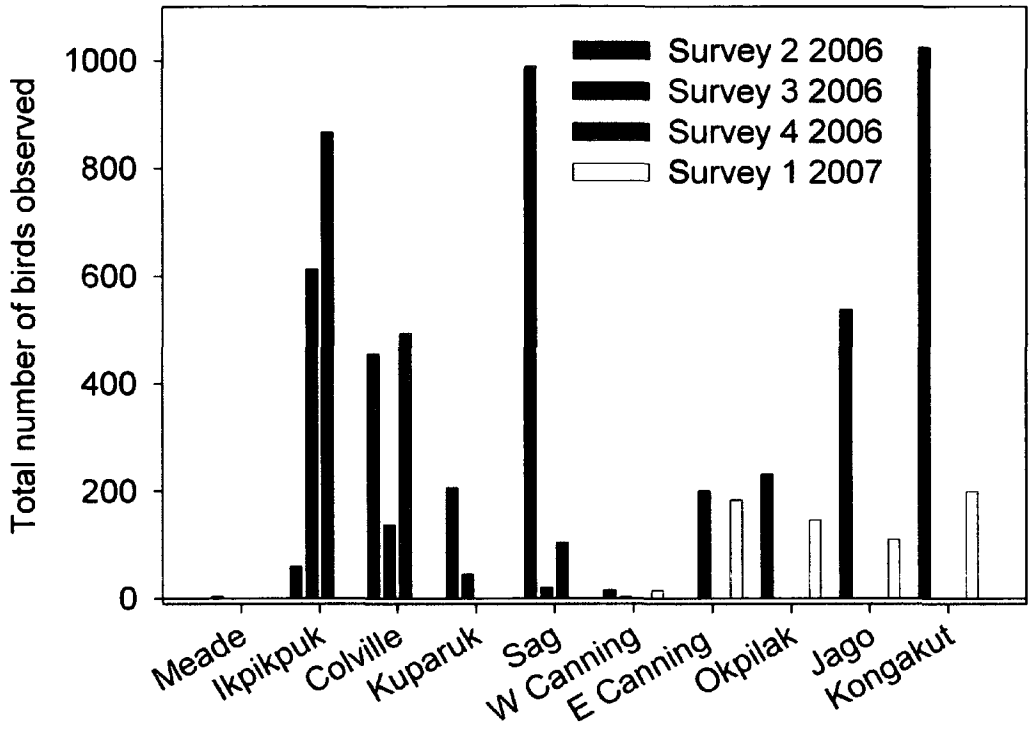
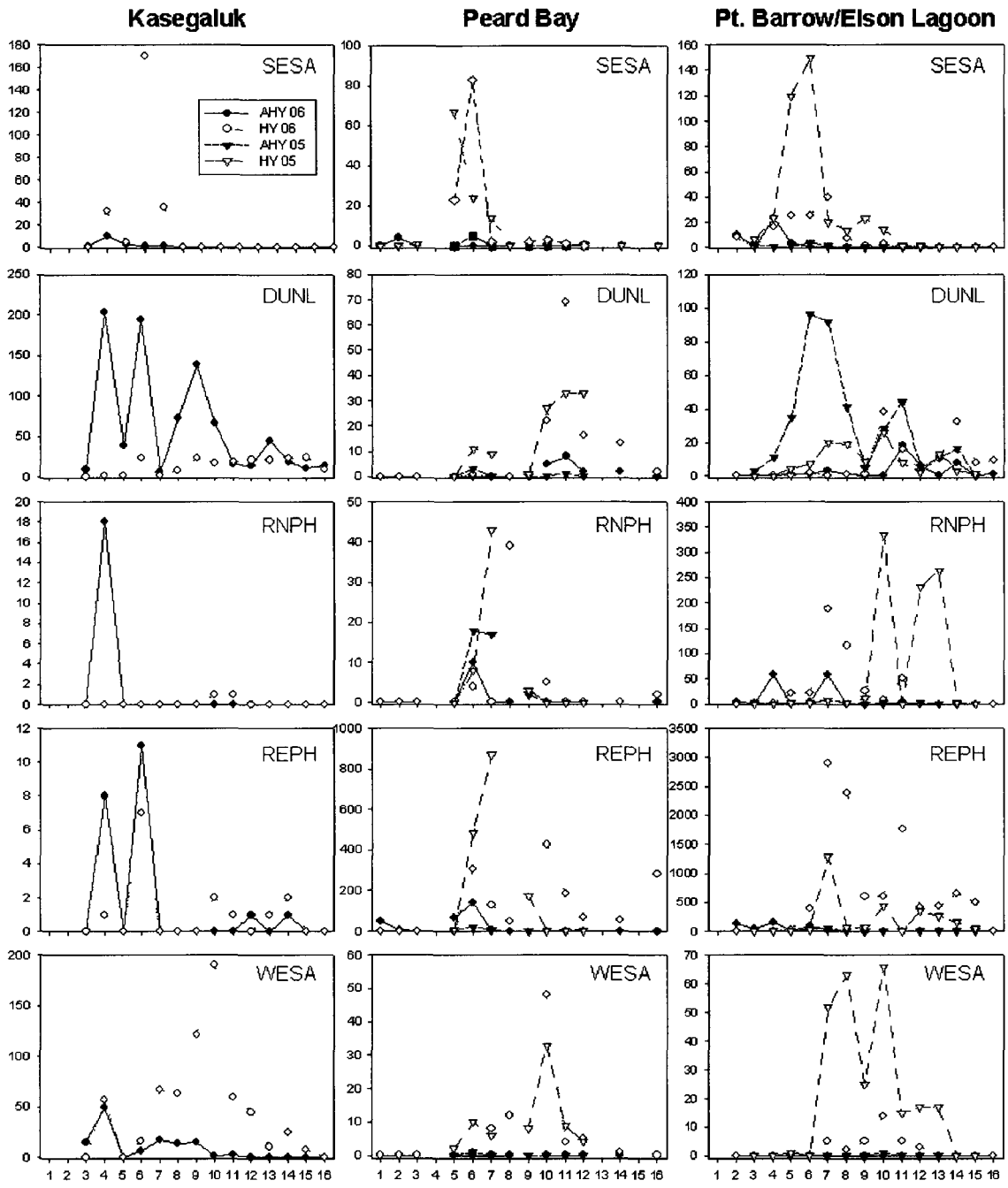


Figure 2.3. Aerial distribution of shorebirds on river deltas in the Beaufort Sea, 2006-2007. Graph shows total number of birds observed per survey for each delta. A lack of bars on the graph for a given survey indicates that no aerial surveys were conducted at that delta in that period. Deltas are listed from west to east along the Beaufort coast and correspond to the gray shaded areas in Figure 2.1. Sag = Sagavanirktok.


Kasegaluk
Peard Bay
Pt. Barrow/Elson Lagoon
SESA
DUNL
RNPH
REPH
WESA
AHY 06
HY 06
AHY 05
HY 05

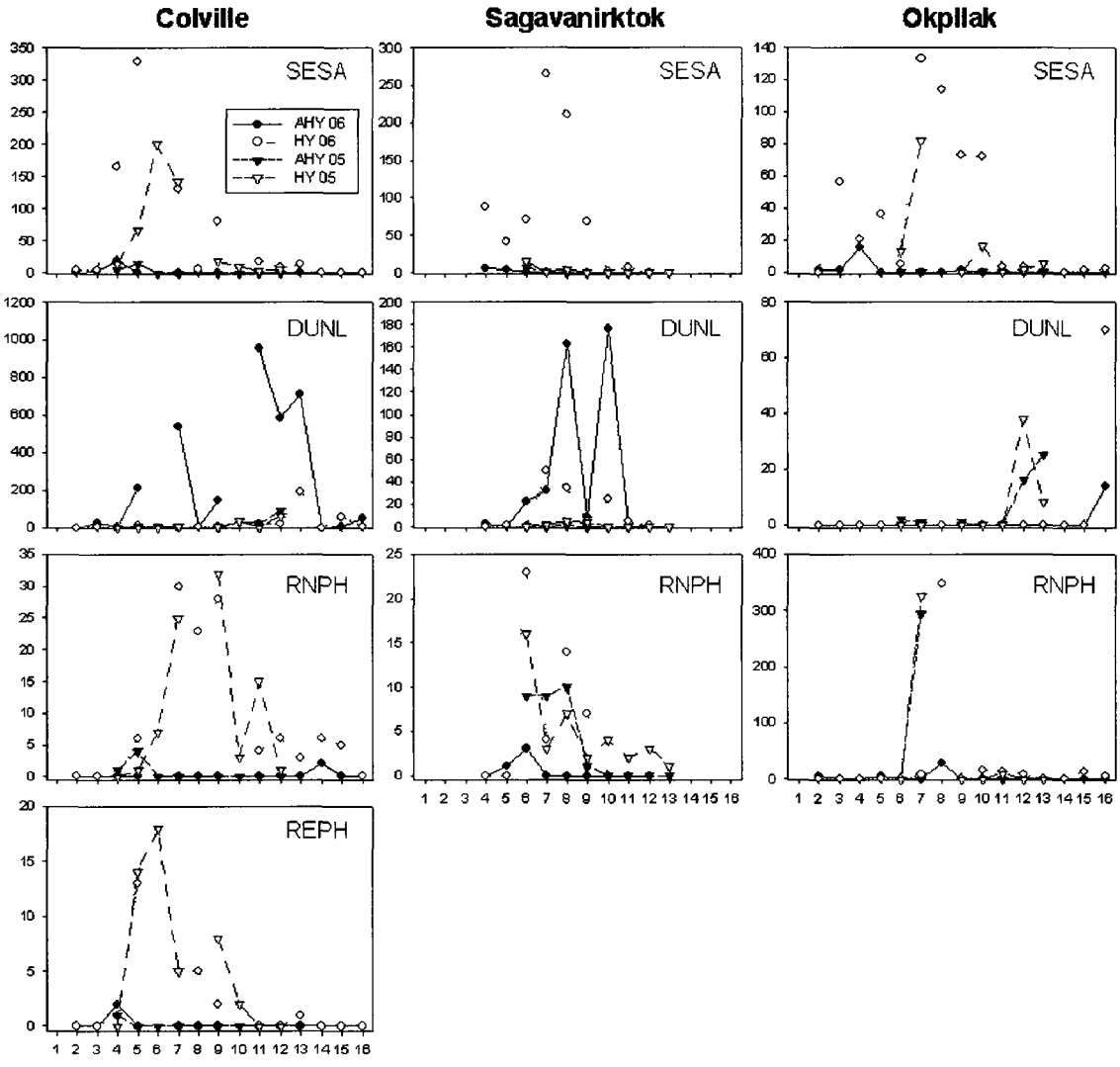
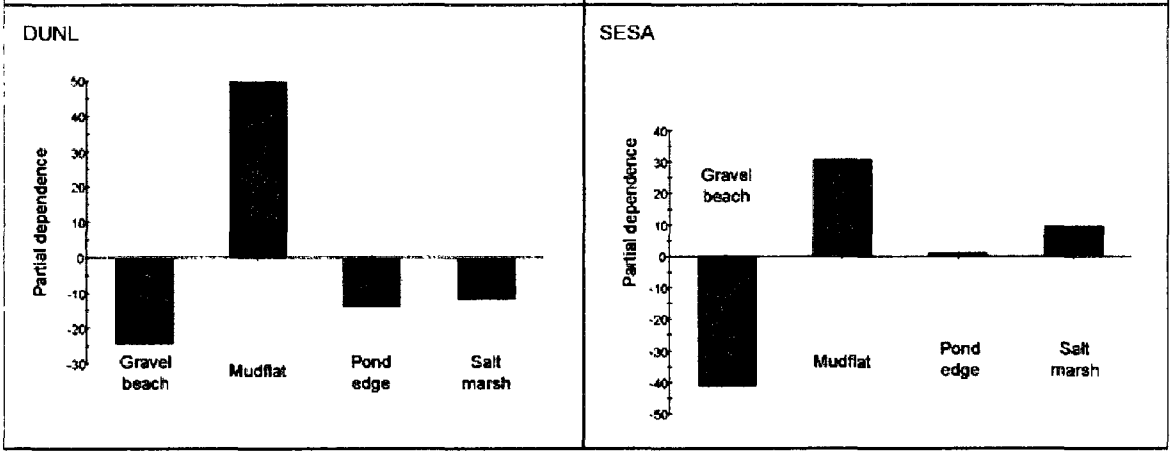
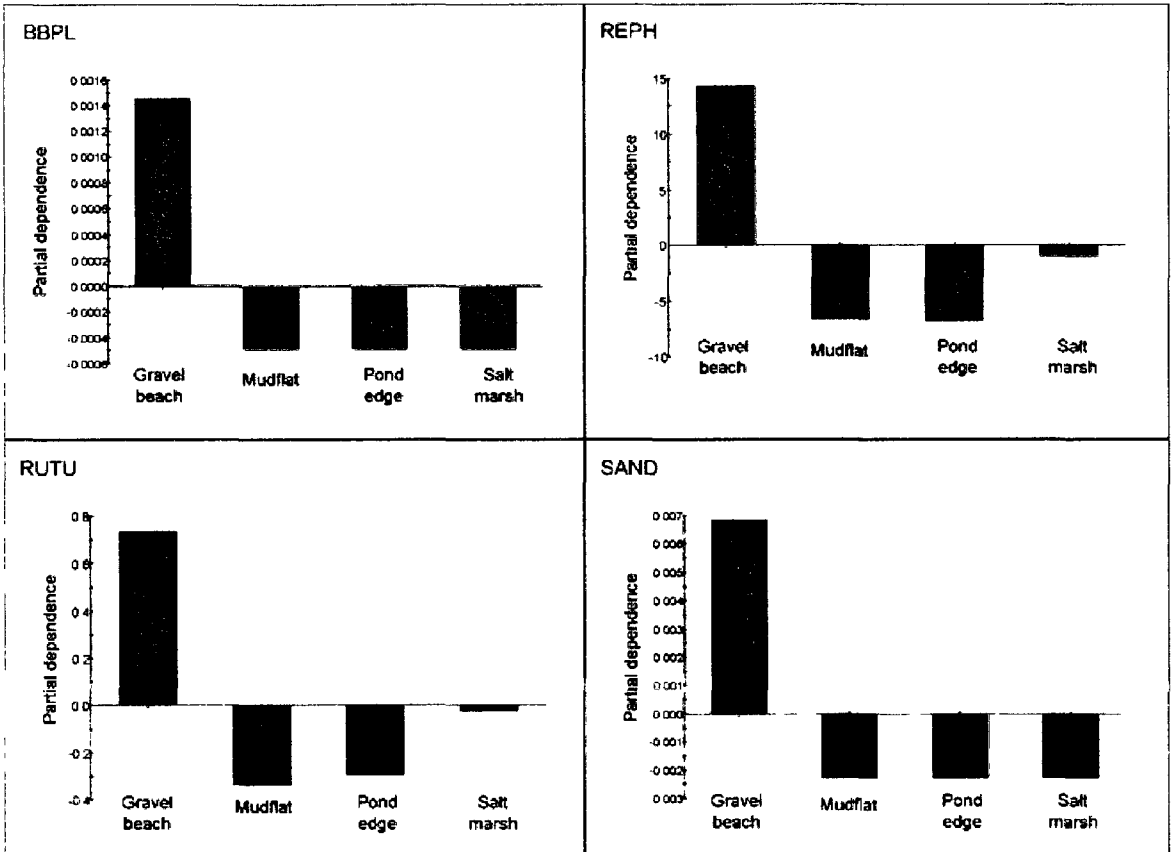

Colville
Sagavanirktok
Okpilak
SESA
DUNL
RNPH
REPH
AHY 06
HY 06
AHY 05
HY 05

Figure 2.4. Raw counts of adults (AHY) and juveniles (HY) of five common shorebird species. Counts are summed across all nine transects within each survey period and location in 2005 and 2006. Camps are listed from west to east along the ACP (see Figure 2.1.). A lack of symbols on the graph for a given survey period indicates that no transect surveys were conducted at that camp in that period. Note that y-axis scale is not the same across the camps. See text for survey period dates. SESA = semipalmated sandpiper, DUNL = dunlin, RNPH = red-necked phalarope, REPH = red phalarope, WESA = western sandpiper.


DUNL
Partial dependence
50
40
30
20
10
0
-10
-20
-30
Gravel beach
Mudflat
Pond edge
Salt marsh
SESA
Partial dependence
40
30
20
10
0
-10
-20
-30
-40
-50
Gravel beach
Mudflat
Pond edge
Salt marsh


BBPL
Partial dependence
Gravel beach
Mudflat
Pond edge
Salt marsh
REPH
Partial dependence
15
10
5
0
-5
-10
Gravel beach
Mudflat
Pond edge
Salt marsh
RUTU
Partial dependence
0.8
0.6
0.4
0.2
0.0
-0.2
Gravel beach
Mudflat
Pond edge
Salt marsh
SAND
Partial dependence
0.007
0.006
0.005
0.004
0.003
0.002
0.001
0.000
-0.001
-0.002
-0.003
Gravel beach
Mudflat
Pond edge
Salt marsh

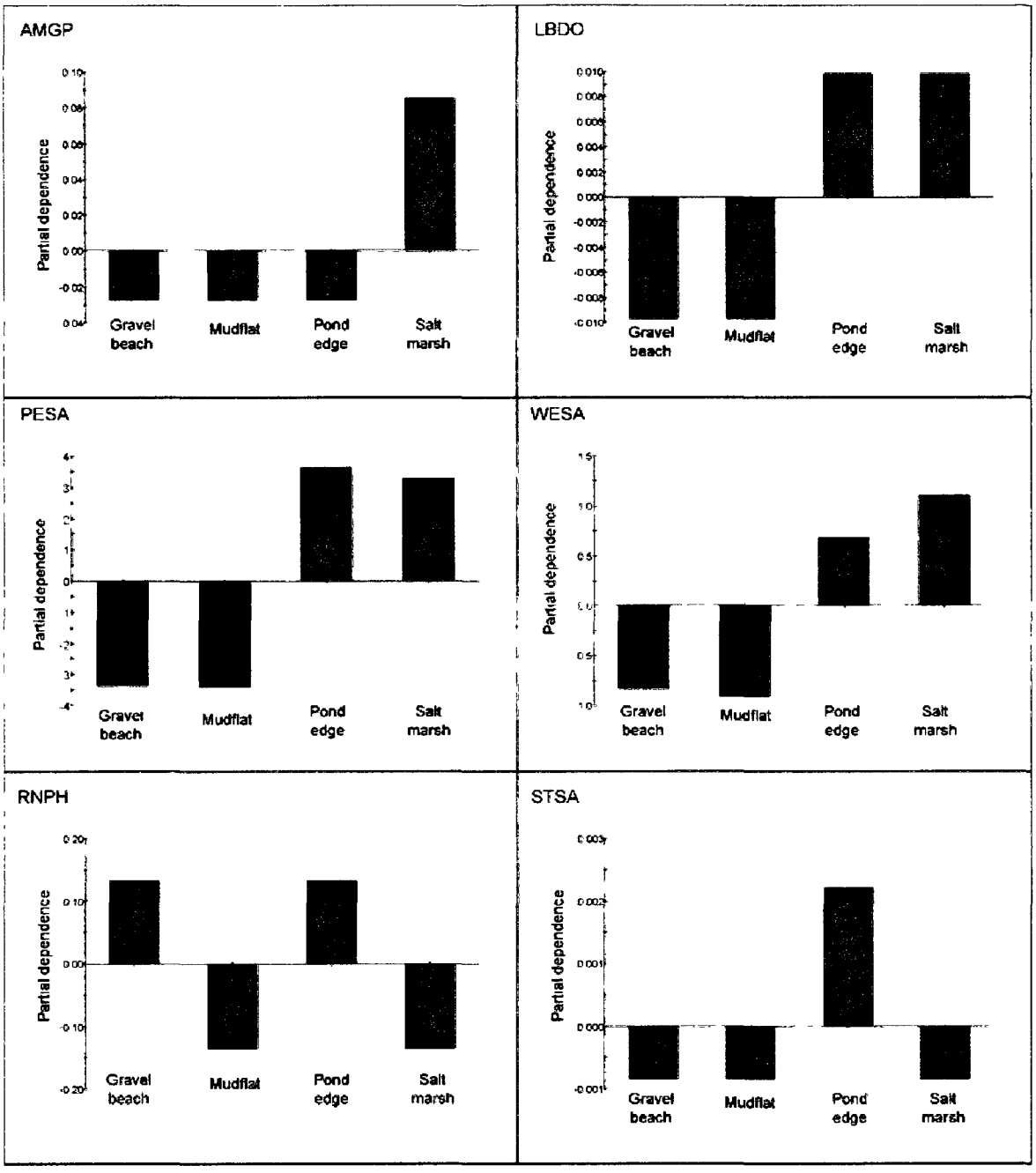

AMGP
Partial dependence
Gravel beach
Mudflat
Pond edge
Salt marsh
LBDO
Partial dependence
Gravel beach
Mudflat
Pond edge
Salt marsh
PESA
Partial dependence
Gravel beach
Mudflat
Pond edge
Salt marsh
WESA
Partial dependence
Gravel beach
Mudflat
Pond edge
Salt marsh
RNPH
Partial dependence
Gravel beach
Mudflat
Pond edge
Salt marsh
STSA
Partial dependence
Gravel beach
Mudflat
Pond edge
Salt marsh

Figure 2.5. Habitat selection by shorebird species at ACP coastal foraging sites. Graphs show partial dependence values indicating the direction of that species' selection for four categories of habitat: gravel beach, mudflat, pond edge, and salt marsh. Larger partial dependence values indicate stronger evidence for selection and/or larger sample sizes. See text for descriptions of habitat type. BBPL = black-bellied plover, REPH = red phalarope, RUTU = ruddy turnstone, SAND = sanderling, DUNL = dunlin, SESA = semipalmated sandpiper, AMGP = American golden-plover, LBDO = long-billed dowitcher, PESA = pectoral sandpiper, WESA = western sandpiper, RNPH = red-necked phalarope, STSA = stilt sandpiper.

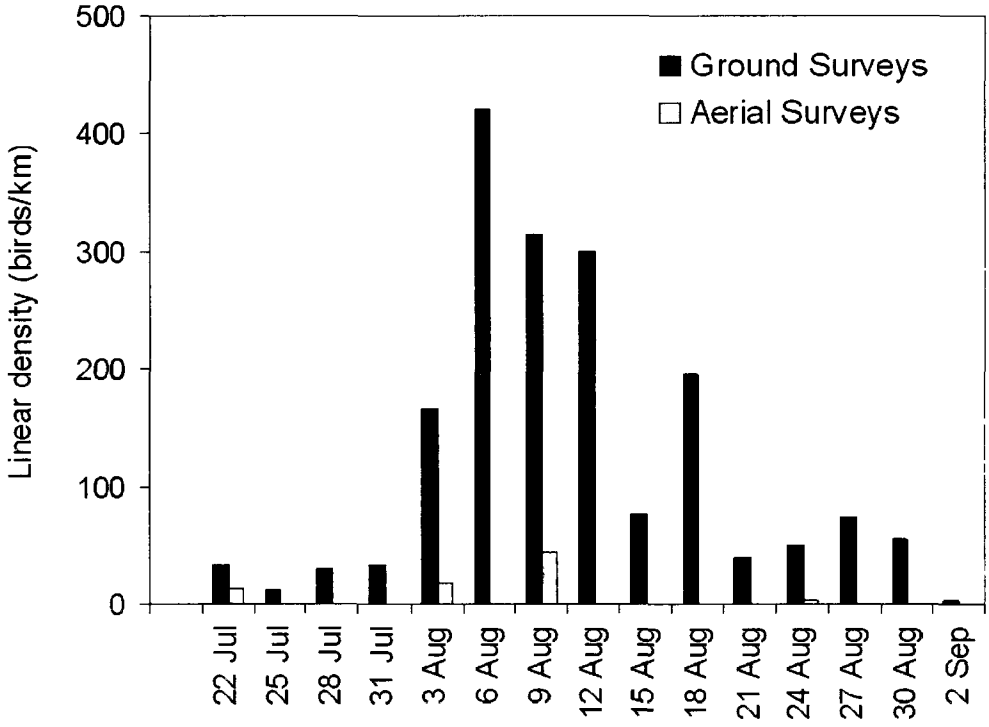


Figure 2.6. Linear densities (birds/km) from aerial and ground surveys for Pt. Barrow/Elson Lagoon in 2006. Dates on x-axis are the last day of each ground transect survey period; one complete survey (nine 1-km transects) was conducted in each period. Aerial surveys in the Pt. Barrow/Elson Lagoon vicinity were conducted on 22 July, 3 August, 9 August, and 23 August 2006.

Table 2.1. Dates and area surveyed for each of six aerial surveys conducted 2005-2007 along the ACP littoral zone. Refer to Figure 2.1. for location of endpoints.

Survey	Aircraft	Dates	Endpoints (W to E)
Survey 1-2005	Helicopter	7-16 August	South end Kasegaluk Lagoon to Demarcation Point
Survey 1-2006	Fixed-wing	22-26 July	Peard Bay to Demarcation Point
Survey 2-2006	Fixed-wing	3-7 August	Kasegaluk Lagoon camp to Demarcation Point
Survey 3-2006	Fixed-wing	9-17 August	South end Kasegaluk Lagoon to Camden Bay
Survey 4-2006	Fixed-wing	23-27 August	South end Kasegaluk Lagoon to Canning River Delta
Survey 1-2007	Fixed-wing	7-8 August	Canning River Delta to Demarcation Point

Table 2.2. Species richness, evenness (E), and Shannon-Weiner diversity index (*H'*) values derived from shorebird transect surveys on the ACP 2005-2006. Results are presented by camp; bolded lines are camps averaged by coast with the relevant camps listed from west to east above each coast. 95% confidence intervals were derived via boot-strap simulations. See Figure 2.1. for camp and coast locations. Pt. Barrow = Pt. Barrow/Elson Lagoon camp; Sag = Sagavanirktok camp. We considered evenness and diversity measures significantly different if the 95% confidence intervals did not overlap.

Year	Coast	Camp	Richness	Evenness (E)	95% CI (E)	Diversity (*H'*)	95% CI (H')
2005	Chukchi	Peard Bay	11	0.4117	0.4111, 0.4123	0.9873	0.9857, 0.9887
		Pt. Barrow	12	0.5283	0.5277, 0.5289	1.3128	1.3114, 1.3142
		Average for Coast	**11.5**	**0.4700**	**0.4420, 0.4980**	**1.1500**	**1.0719, 1.2282**
	Beaufort	Colville	14	0.5732	0.5726, 0.5738	1.5128	1.5114, 1.5142
		Sag	10	0.5762	0.5756, 0.5768	1.3267	1.3253, 1.3282
		Okpilak	13	0.5051	0.5045, 0.5057	1.2955	1.2941, 1.2969
		Average for Coast	**12.3**	**0.5515**	**0.5390, 0.5640**	**1.3783**	**1.3419, 1.4148**
2006	Chukchi	Kasegaluk	8	0.6175	0.6172, 0.6177	1.2840	1.2834, 1.2846
		Peard Bay	10	0.3698	0.3695, 0.3700	0.8514	0.8508, 0.8520
		Pt. Barrow	14	0.1407	0.1404, 0.1409	0.3713	0.3707, 0.3719
		Average for Coast	**10.7**	**0.3760**	**0.3020, 0.4499**	**0.8356**	**0.6940, 0.9771**

Table 2.2 continued.

Beaufort	Colville	12	0.3256
	Sag	8	0.5927
	Okpilak	11	0.5567
	Average for Coast	**10.3**	**0.4917**

0.3253, 0.3259	0.8091	0.8085, 0.8097
0.5924, 0.5929	1.2325	1.2319, 1.2330
0.5564, 0.5570	1.3349	1.3344, 1.3355
0.4467, 0.5366	**1.1255**	**1.0391, 1.2119**

Table 2.3. Raw counts for five common shorebird species observed on survey transects at each ground camp on the ACP 2005-2006. Observations from all survey periods in each year are lumped. Camps are listed from west to east across the ACP. For each camp, the first line for each species shows the count for that species and the percent of total (in parentheses), which refers to the proportion of the total observations summed across all five species each species comprised. The second two lines show the counts for adult (AHY) and juvenile (HY) individuals for each species. SESA = semipalmated sandpiper, DUNL = dunlin, RNPH = red-necked phalarope, REPH = red phalarope, WESA = western sandpiper.

	Chukchi Sea					Beaufort Sea					
	Kasegaluk Lagoon	Peard Bay		Pt Barrow/Elson Lagoon		Colville Delta		Sag Delta		Okpilak	
Species	2006	2005	2006	2005	2006	2005	2006	2005	2006	2005	2006
SESA	**262 (2.2)**	**119 (6.0)**	**110 (4.5)**	**377 (7.8)**	**161 (1.3)**	**480 (53.7)**	**787 (17.5)**	**29 (26.9)**	**766 (56.9)**	**118 (14.0)**	**537 (49.9)**
AHY	18	5	4	7	36	19	25	8	11	0	18
HY	244	114	106	370	125	461	762	21	755	118	519
DUNL	**1038 (53.9)**	**118 (6.0)**	**142 (5.8)**	**499 (10.3)**	**159 (1.3)**	**277 (31.0)**	**3565 (79.3)**	**12 (11.1)**	**528 (39.2)**	**91 (10.8)**	**84 (7.8)**
AHY	848	4	17	387	39	162	3242	1	406	45	14
HY	190	114	125	112	120	115	323	11	122	46	70
RNPH	**20 (1.0)**	**91 (4.6)**	**62 (2.5)**	**873 (18.1)**	**565 (4.7)**	**89 (10.0)**	**113 (2.5)**	**67 (62.0)**	**52 (3.9)**	**632 (75.1)**	**456 (42.3)**
AHY	18	37	10	18	132	5	2	29	4	295	41
HY	2	54	52	855	433	84	111	38	48	337	415
REPH	**35 (1.8)**	**1580 (79.8)**	**2058 (84.0)**	**2827 (58.5)**	**11175 (92.4)**	**48 (5.4)**	**29 (0.6)**	**0**	**0**	**0**	**0**
AHY	21	35	269	114	502	1	2	0	0	0	0
HY	14	1545	1789	2713	10673	47	27	0	0	0	0
WESA	**791 (41.1)**	**73 (3.7)**	**79 (3.2)**	**257 (5.3)**	**34 (0.3)**	**0**	**0**	**0**	**0**	**0**	**0**
AHY	125	1	0	1	0	0	0	0	0	0	0
HY	666	72	79	256	34	0	0	0	0	0	0
TOTAL	*2146*	*1981*	*2451*	*4833*	*12094*	*894*	*4494*	*108*	*1346*	*841*	*1077*

Table 2.4. Raw counts for less common shorebird species observed on survey transects at each ground camp on the ACP 2005-2006. Observations from all survey periods are lumped within each year, as are adults and juveniles. Camps are listed from west to east across the ACP. AMGP = American golden-plover, BASA = Baird's sandpiper, BBPL = Black-bellied plover, BBSA = buff-breasted sandpipers, LBDO = long-billed dowitcher, PESA = pectoral sandpiper, RUTU = ruddy turnstone, SAND = sanderling, SEPL = semipalmated plover, STSA = stilt sandpiper.

	Chukchi Sea					Beaufort Sea					
	Kasegaluk Lagoon	Peard Bay		Pt. Barrow/Elson Lagoon		Colville Delta		Sag Delta		Okpilak	
Species	2006	2005	2006	2005	2006	2005	2006	2005	2006	2005	2006
AMGP	4	3	1	0	2	42	15	0	18	27	30
BASA	0	0	1	3	27	2	0	2	0	1	0
BBPL	0	0	0	1	10	55	16	0	53	52	70
BBSA	0	0	0	0	1	15	2	0	0	5	0
LBDO	17	20	46	9	3	9	11	6	0	6	0
PESA	59	12	5	29	25	66	65	221	39	30	56
RUTU	0	10	0	50	40	22	15	10	0	20	33
SAND	0	20	29	16	2	1	0	0	0	102	47
SEPL	0	1	0	1	13	0	0	1	0	0	1
STSA	0	0	0	0	0	117	61	3	338	11	9
TOTAL	*80*	*66*	*82*	*109*	*123*	*329*	*185*	*243*	*448*	*254*	*246*

3. RESIDENCE TIME AND MOVEMENTS OF POSTBREEDING SHOREBIRDS ON THE NORTHERN COAST OF ALASKA[1]

3.1. Abstract

Relatively little is known about shorebird movements across the coast of northern Alaska, yet this coastline is used extensively by postbreeding shorebirds prior to fall migration. We deployed 354 radio transmitters on breeding (n = 153) and postbreeding (n = 201) shorebirds of five species in 2005-2007. We made two *a priori* predictions: (1) postbreeding movements should reflect ultimate southbound migration routes, and (2) either migration strategy (length of flight bouts) or timing of molt in relation to migration (molt occurring at breeding vs. wintering areas) would be most influential in determining behavior of postbreeding shorebirds. Semipalmated Sandpipers moved eastward, consistent with their ultimate migration direction; movement patterns of other species did not support our first prediction. Timing of postnuptial molt appeared to have more influence over residence time and movements than did migration strategy. Post-capture residence time for Semipalmated Sandpipers was less than for Western Sandpipers and significantly less than for Dunlin, and movements between sites occurred more quickly and frequently for Semipalmated Sandpipers than Dunlin. We expected to see the opposite patterns if migration strategy were more influential. Our data shed light on how

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different shorebird species use the northern Alaska coast after breeding: most species are likely to be stopping over at postbreeding areas, whereas Dunlin and some Western Sandpipers may be staging. We suggest the coast of northern Alaska be viewed as an interconnected network of postbreeding sites that serve multiple breeding shorebird populations.

Key Words: Arctic, migration, spatial connectivity, staging, stopover, telemetry, waders

3.2. Introduction

Patterns of migratory bird abundance and distribution across a large geographic area are challenging to interpret unless the propensity for individuals to enter, leave, or change locations within that area is understood. Additionally, movements of individuals within or between seasons may link habitats at a regional level (Plissner et al. 2000). Therefore landscape connectivity, as defined by migratory movements, is an important consideration in the development of area-wide conservation strategies (Haig and Oring 1998). Within a community of organisms, even where all members appear to be using identical sites or habitats, species may move across the landscape at different temporal and spatial scales (Naugle et al. 1999). Thus it is critical that species-specific residence and movement patterns are compared and contrasted prior to identifying key conservation sites, ranking areas by importance, or developing region-wide management strategies.

Alaska's northern coast is a vast expanse of low-lying tundra bordered to the north and west by the Beaufort and Chukchi Seas, and to the east by Canada (3.1). After the breeding season but prior to fall migration, shorebirds congregate on the northern coast of Alaska in relatively high densities (Connors et al. 1981, Connors 1984, Taylor et al. 2010). Dominant species include Semipalmated Sandpiper (*Calidris pusilla*), Dunlin (*Calidris alpina arcticola*), Red Phalarope (*Phalaropus fulicarius*), Red-necked Phalarope (*Phalaropus lobatus*), and Western Sandpiper (*Calidris mauri*). Given the potential for rapid environmental change in the Arctic due to industrial development and accelerated warming (Gilders and Cronin 2000, IPCC 2001), knowledge of the numbers of shorebirds using the coast of northern Alaska during the postbreeding period is critical for assessing potential effects of environmental and human-mediated change. Two important parameters to consider in estimating population size is whether individuals use one or multiple locations while preparing for fall migration, and how long they remain at each site. These variables also affect our understanding of whether shorebird species are actually staging on the coast of northern Alaska (i.e. acquiring fat resources needed for migratory flight) or are simply using the region as a temporary rest stop between breeding activities and southbound flight. The need for making a clear distinction between sites where staging vs. stopping over occurs has been recently highlighted by Warnock (2010). Information on residence time and speed at which postbreeding shorebirds move between sites is also important for designing coastal monitoring programs and for informing biological assessments addressing the cumulative impacts to migratory birds of industrial

development along the northern Alaska coast (World Wildlife Fund/Audubon Alaska 2007).

Because few studies of marked shorebirds have been conducted across the northern Alaska coast, we lack information on how long different species remain at postbreeding sites, and how they move between breeding and postbreeding areas or subsequent postbreeding sites. It is likely that life history characteristics of each species dictate these movement patterns. In this paper we examined two hypotheses about species-specific residence and movement patterns arising from (a) differences in migratory routes, and (b) variation in molt/migration strategies. We hypothesized that shorebirds' direction of movement during the postbreeding period should be reflective of their ultimate southbound migration route for two reasons. First, movements during the postbreeding period may not be entirely distinct from migratory movements depending on whether individuals are using sites for staging or just stopping over. Second, Arctic-breeding shorebirds face rapid deterioration of weather conditions and food availability in late summer (Bonier et al. 2007); thus it may be advantageous for these species to minimize time and energy spent traveling in a non-migratory direction. Semipalmated Sandpipers breeding in northern Alaska are thought to migrate south through the central prairies of Canada and the U.S. (Harrington and Morrison 1979, Hicklin and Gratto-Trevor 2010), thus their predominant direction of movement in northern Alaska is likely to be eastward. In contrast, a pattern of westward movement is likely for the *arcticola* subspecies of Dunlin, which is believed to migrate first to western Alaska, then across the

Bering Sea to eastern Asia (Gill 1996, Warnock and Gill 1996, Fernández et al. 2008). Red and Red-necked Phalaropes are also likely to move west along the coast of northern Alaska because their ultimate migration route is probably south through the Bering Sea to the Pacific Ocean (Rubega et al. 2000, Tracy et al. 2002). Although there is little information published on Red-necked Phalaropes, Watson and Divoky (1974) reported seeing Red Phalaropes in northern Alaska moving westward past Point Barrow during fall migration.

The second question we examine in this paper is whether post-capture residence time and the speed and timing of postbreeding movements are more affected by species-specific migration strategies (short vs. long hop flights) or the timing of post-nuptial molt relative to fall migration (molt before vs. after migration). Piersma (1987) described three different migration strategies employed by long-distance migrants based on distances traveled between flights: "hop" and "skip" migrants that undertake short or intermediate flights, respectively, and "jump" migrants that undertake longer flights, often over an ecological barrier. Warnock (2010) suggested that hop and skip migrants have less need for large fuel reserves, thus spend less time at foraging areas prior to or during migration (merely "stopping over"), whereas jump migrants "stage" for longer periods at postbreeding foraging areas in order to accumulate necessary fuel reserves prior to starting migration.

Regardless of migratory bout length, for species that migrate away from breeding areas and molt on the wintering grounds, early departure from breeding areas may mean

earlier arrival at the southern terminus of migration. This may confer an advantage if it reduces competition for food resources during molt (O'Hara et al. 2002) or enables individuals to avoid migrating at the same time as major predators (e.g. falcons: Butler et al. 2003, Lank et al. 2003, Ydenberg et al. 2007). In contrast, species that molt on the breeding grounds prior to fall migration have less demand for resources on the wintering grounds (they are not undergoing molt and recovering from migration) and may opt to remain in the Arctic longer. Individuals of these species may also be constrained by their ability to acquire the fat resources necessary for migration while simultaneously regrowing feathers, particularly as juveniles (Lindstrom et al. 1994, Bonier et al. 2007), so preparation for migration prior to leaving the Arctic could be a lengthier process.

In northern Alaska, the suite of calidridine sandpipers that are commonly found together at coastal foraging sites exemplify the differences in migration strategies and timing of molt. Semipalmated Sandpipers are known long-jump migrants that cross the Atlantic Ocean on their way to wintering areas in north and central South America (Wilson 1994, Hicklin and Gratto-Trevor 2010). They typically migrate to tropical wintering areas first, then undergo complete prebasic molt (Holmes 1972, Prater et al. 1977). Dunlin (*arcticola* subspecies) are short- to intermediate-distance migrants that undergo wing and body feather molt in the Arctic during and shortly after the breeding season (Holmes 1971, Warnock and Gill 1996). Western Sandpipers are short-hop migrants (Iverson et al. 1996) that may begin prebasic body feather molt in the Arctic but

complete flight feather molt at wintering areas; some individuals may arrest body molt during fall migration (Wilson 1994).

The predicted influence of these differences in migration strategies vs. molt in relation to migration timing on behavior of postbreeding shorebirds in northern Alaska is contradictory. Theoretically, Semipalmated Sandpipers should stage on the northern coast of Alaska as a result of their long-jump strategy, yet they may also be under selection to migrate south relatively quickly given that they must molt when they reach wintering areas. In contrast, Dunlin should be less likely to actually stage in northern Alaska given their short- or intermediate-hop migration strategy, but the result of their molting in the Arctic prior to migrating south may be to lengthen their time at postbreeding foraging areas. Western Sandpipers are likely to exhibit an intermediate strategy: given their short-hop migration strategy they are likely to exhibit stopover behavior (not staging) at northern Alaska foraging areas, but the variable timing of molt relative to migration dictates that individuals may adopt different departure strategies depending on when they begin post-nuptial molt. We hypothesized that differences in one of these life history traits (migration strategy vs. timing of molt relative to migration) would be more influential than the other in terms of structuring postbreeding movements of calidrids in northern Alaska.

Using radio telemetry detections of birds at and away from their initial capture sites, we examined these hypotheses by documenting residence time and movement direction, speed, and timing for five dominant shorebird species (prediction 1) or three

calidrid species (prediction 2) on the northern Alaska coast during the postbreeding period. We also report observational data on movements of radio-equipped Semipalmated Sandpipers and Dunlin away from the coast of northern Alaska. Because we used VHF-based radio telemetry over a large area, we advise the reader upfront that our results are based on limited sample sizes and therefore may not be generalizable to all individuals of each species.

3.3. Methods

We studied movement patterns of postbreeding shorebirds along the northern coast of Alaska from 2005-2007. The habitat in this area is a complex mosaic of brackish water mudflats and marsh; low-lying saline tundra; mud and gravel shores of sloughs, river deltas, and lagoons; and gravel mainland and barrier island beaches within 100-1000 m of the coastline (Johnson and Herter 1989). Birds were equipped with transmitters at capture locations and subsequently detected (defined as hearing a radio signal) using a combination of manual telemetry, automated telemetry stations (ARTS), and aerial surveys conducted across the northern Alaska coast during the staging period (late July-early September). Capture locations were established based on (a) the presence of either a large lagoon system (Peard Bay, Barrow, Kasegaluk) or a large river delta (Ikpikpuk, Colville, Sagavanirktok, Canning, Okpilak), both of which support large numbers of staging shorebirds, (b) the potential for logistical support from other project collaborators

for conducting work at the site, and (c) the ability to access the sites with a boat, helicopter, or fixed-wing aircraft. Locations and dates of activity for radio deployment, monitoring sites, and ARTS varied slightly among and between years (Table 3.1, Fig. 3.1).

We captured adult (AHY) shorebirds on nests during the breeding period (15 June-15 July) in 2005-2007, and juvenile shorebirds (HY) and a small number of adults at coastal areas during the postbreeding period (16 July-1 September) in 2005-2007 (Table 3.2). Captured individuals in healthy condition (i.e., alert, normal weight, good feather condition) were fitted with radio transmitters (2005: model A2400 series, 1.0-1.7 g, Advanced Telemetry Systems, Inc., Isanti, MN; 2006 and 2007: model BD-2, 0.9-1.6 g, Holohil Systems Ltd., Ontario, Canada; all with lifespan of 7-11 weeks depending on model). To equip birds with transmitters, we first clipped all body feathers from an area slightly larger than the size of the transmitter approximately 1 cm anterior to the uropygial gland. Next we attached the transmitter using superglue and a spray-on catalyst (Loctite 454 Prism Instant Adhesive and 7452 Accelerator). Previous research indicated that retention time for transmitters attached with this method was at least seven weeks (Warnock and Warnock 1993). Because we wished to track Dunlin after they left northern Alaska and migrated to staging areas in western Alaska, we attached their transmitters using both glue and a leg-loop harness made of 1-mm thick, stretchable beading cord (StretchMagic brand, Pepperell Braiding Company, Inc.; Sanzenbacher et al. 2000). All birds were released at their capture site after radio attachment, usually

within 30 minutes of capture. All shorebird capture activities were conducted under a University of Alaska Fairbanks Institutional Animal Care and Use Committee protocol (#04-31).

We monitored movements of radio-equipped shorebirds using several different methods. First, personnel at each field camp delineated a 10-km diameter study area that encompassed several banding sites and known shorebird foraging locations. Within this area, personnel listened for frequencies from all capture locations approximately every other day using hand-held yagi antennas and ATS R4000 radio receivers. While conducting manual telemetry searches at ground level, our detection distance for radio-equipped birds was 0.5-1 km (based on tests locating known and hidden transmitters within the study area). Second, ARTS were established at each of the field camps and at accessible coastal or inland locations at the remote sites. The ARTS were comprised of two 4-element yagi antennas situated 90° apart at the top of a 6m tower. Antennas were pointed along the coast to maximize coverage of the predicted flight path of migrating shorebirds. Detections of radio-equipped birds were recorded by an ATS R4500 receiver, programmed to continuously scan frequencies from all deployment locations 24 hours per day. A reference transmitter was placed near each ARTS to verify that the receiver was working throughout the study period. The detection distance for radio-equipped birds by the ARTS was estimated to be 2-3 km, based on detections of transmitters being moved along the coast into and out of range of the receiver. Third, we listened for radio-equipped birds from the air during surveys conducted along the coastline of the study

area every two weeks (weather permitting) from mid-July to late August (Taylor et al. 2010). We flew surveys from Kasegaluk Lagoon to the Canadian border by Demarcation Point (designated by vertical lines on left and right side of map in Fig. 3.1) in 2005 and 2006, and from the Canning Delta to Demarcation Point in 2007 (from 9,G to right side of map in Fig. 3.1). Survey aircraft were equipped with H-antennas and ATS R4000 receivers, which were used to scan all possible frequencies continuously while in flight. Detections of the ARTS reference transmitters enabled us to verify that our aircraft receivers were functioning. Finally, personnel at the Yukon Delta National Wildlife Refuge listened for radio-equipped Dunlin during five aerial surveys conducted in 2005 (26 August, 20 and 30 September, 4 and 7 October 2005) along the outer coast of the central Yukon-Kuskokwim Delta (YKD). Although the YKD is believed to be an intermediate staging location for migrating Dunlin that breed in northern Alaska and winter in Asia (Warnock and Gill 1996), little is known about how Dunlin move between northern Alaska and the YKD.

3.3.1. Statistical Analyses

We examined the directionality of movements > 5 km in length to examine our first hypothesis that a species' direction of movement should be reflective of their ultimate migration route. We considered these movements to be indicative of birds traveling to locations other than their initial capture site because a bird moving 5 km or more from its initial capture location would no longer be detected in the original study area. In reality,

most movement segments were at least 50 km in length. We considered each individual only once in the analysis by using the detection that represented the farthest distance the bird moved from its initial capture location. For birds that left a study area and returned multiple times, we only counted the movement that the individual took after leaving the study area for the last time. We combined data for each species across all three years due to low sample sizes within a given year. Where sample sizes were sufficient, we calculated the mean vector (degrees) and mean distance moved (km) for AHY birds captured at nest sites using circular statistics in Oriana Version 2.02c (Kovach Computing Services 2005). We did not calculate mean distance moved for HY birds because these birds were all captured at postbreeding locations (i.e., we did not know where their natal location was and thus could not determine how they moved from nest sites to postbreeding sites). We also calculated the number of days between when the radio-equipped individual was last detected at its capture location and when it was first detected at a new location, and the minimum distance traveled from nest locations for individual adults captured at breeding sites.

We examined our second hypothesis (that post-capture residence time and the speed and timing of postbreeding movements should differ based on either species' migration strategies or postnuptial molt schedules) by evaluating subsequent detections of the same individual. This was done either (a) at an individual's capture site to estimate residence time, or (b) between the capture site and subsequent sites to assess whether movements of birds between sites represented directional migratory movements or

staging at one or more sites. Individuals detected at one or more sites for one to a few days and moving in a linear pattern along the coastline were considered to have exhibited directional migration (any halts in migration are likely stopovers), whereas detections of individuals at one or more sites for a week or more were considered as possibly staging at a site.

To calculate residence time for each species, we used mark-recapture analysis methods implemented in Program MARK (White and Burnham 1999). We first created encounter histories for each radio-equipped bird that was detected more than once at its capture site, with a "1" denoting the individual being detected on a given day at the site, and a "0" denoting failure to detect that individual on a given day. We combined data from both manual and ARTS telemetry efforts, such that a 1 in the encounter history reflected presence detected by either method while a 0 reflected lack of detection by either method. We used the Cormack-Jolly-Seber (CJS) open-population model framework to analyze these encounter histories by examining the weight of evidence in the data for each of a candidate set of models explaining two modeled response parameters: Φ (survival probability), and p (detection probability). Our set of candidate models included keeping response parameters constant (dot models) vs. allowing survival and/or detection probability to vary across species, across time with a linear or quadratic trend, or with an interaction between species and individual day captured. Our models also included a suite of daily covariates for each camp that indicated whether camp personnel were actively listening for radio-equipped birds or if only the ARTS were

capable of detecting a radio-equipped bird on that date. $QAIC_c$ (Akaike's Information Criterion adjusted for small sample sizes and lack of model fit) and the associated $\Delta QAIC_c$ and Aikaike weights for each model were used as model selection criteria (Burnham and Anderson 2002). We transformed the survival estimates obtained from Program MARK into post-capture residence times according to the following formula for life expectancy (Kaiser 1995):

$$\text{residence time} = -1/\ln(\Phi)$$

For all descriptive statistics of movement patterns, we report mean ± SD.

3.4. Results

We radio-equipped 139 Semipalmated Sandpipers, 91 Dunlin, 65 Red Phalaropes, 41 Red-necked Phalaropes, and 18 Western Sandpipers at breeding and postbreeding locations in 2005-2007 (Table 3.2). Of these individuals, 196 (55%) were detected multiple times at their capture locations and used to assess post-capture residence time, and 45 (13%) were subsequently detected at sites other than their capture location and were used to assess movement patterns. The majority of these 45 individuals were detected at only one location subsequent to their capture site; nine were detected at two sites, and two were detected at three sites. Birds captured at nest sites during the breeding season were detected at a slightly lower rate than birds captured during post-

breeding (11% vs. 14%). Eighty-five percent of detections were made by the ARTS, 10% by aerial telemetry, and 5% by manual telemetry.

3.4.1. Length and direction of movements away from capture sites

We detected 31 of 139 Semipalmated Sandpipers (13 AHY, 18 HY) after initial capture, which represented the highest recovery rate for all species (22% versus 7-8% for the other species). Most (27 of 31) Semipalmated Sandpipers of both age groups moved eastward. This was the only species for which we had sufficient sample size to calculate a mean movement vector: for eleven adults in 2005-2006 this vector was 97.0° ± 31.4°. Both age groups displayed a distinct pattern of movement northeast along the Chukchi coast (if initially captured there), then east along the Beaufort coast (Fig. 3.2). Eleven of the 13 AHY birds were captured at tundra nesting sites and were later detected on the coast. Time between initial capture and subsequent detection averaged 16.0 ± 7.1 days for these individuals, and they exhibited an average movement of 137.2 ± 129.6 km between detections. Two AHY and 18 HY Semipalmated Sandpipers were initially captured on the coast during postbreeding, and were later detected having moved to different coastal sites between <1 and 14 days later (mean 4.5 ± 3.9 days). Eight individuals were detected multiple times, each time farther north along the Chukchi coast or farther east along the Beaufort coast (Table 3.3). For six of these eight birds the length of time between successive detections was a single day or less, despite most travel distances being approximately 100 km or greater. These individuals in particular indicate

that Semipalmated Sandpipers tend to move rapidly along the northern Alaska coast during the postbreeding period.

Semipalmated Sandpipers appeared to have an affinity for migrating to the vicinity of the Canning River Delta (Fig. 3.2). Twenty-two of 31 individuals (71%) that were detected away from their capture sites were detected at either the Canning River Delta (G; 17 individuals) or at an ARTS along the Canning River (H; 5 individuals). This included 11 AHY and 11 HY birds captured initially at breeding sites and at coastal postbreeding areas, respectively. None of these individuals were subsequently detected at the Okpilak Delta (I), farther east along the Beaufort coast. Additionally, two AHY Semipalmated Sandpipers initially captured while breeding at East Arey Lagoon (11) moved in an opposite direction of most of the other birds (i.e., west) toward the Canning River: one was detected at the Canning River Delta, and the other at the Okpilak Delta.

We detected six of 77 Dunlin (8%, 4 AHY, 2 HY) on the northern Alaska coast after initial capture. Three Dunlin traveled southwest while three others traveled northeast and east (Fig. 3.2). Two of the AHY Dunlin were radio-equipped at their nest sites 80 m apart in Barrow (4) on the same day. Both individuals were detected 56 days later southwest of their initial capture site at Peard Bay (B). The third AHY Dunlin was captured at a nest 23 km south of Peard Bay (2), and was detected 51 days later having moved eastward to Barrow (C). The fourth AHY Dunlin was captured at a nest 6 km west of Prudhoe Bay (8) and was detected 70 days later after moving east to the coast at the Sagavanirktok Delta (F). These four adult Dunlin moved 56.9 ± 39.9 km between

breeding territories and where they were detected during postbreeding, and were first detected 53.0 ± 13.7 days after initial capture at nest sites. One of the two HY Dunlin was initially captured while Barrow (C); it moved southwest to Peard Bay (B), arriving three days after it was last detected in Barrow. The second HY bird moved from its initial capture location at Kasegaluk Lagoon (A) northeast to Barrow (C), and was detected there 18 days after its last detection at Kasegaluk Lagoon.

Seven of the 24 Dunlin (29%; 4 AHY, 3 HY) that were radio-equipped in 2005 were later detected via aerial telemetry on the YKD between 26 August and 7 October 2005 (Table 3.4). Three of the AHY Dunlin had last been detected at their breeding sites on the ACP in late June or early July prior to being detected on the YKD between 20 September and 7 October. The fourth AHY individual was radio-equipped on a nest in Barrow on 1 July, subsequently detected in Barrow on 1 August, and finally detected on the YKD on 4 October. The three HY individuals were captured at the Colville Delta and Barrow, and were last detected on the northern Alaska coast in mid- to late August. One was subsequently detected on the north side of the YKD ten days after last being heard on the northern Alaska coast (indicating relatively rapid movement southward after departure from northern Alaska), while the other two were detected on the YKD in late September.

We detected five of 65 Red Phalaropes (8%; 1 AHY, 4 HY) after their initial capture. Red Phalaropes moved primarily to the northeast and southwest during the postbreeding period (Fig. 3.2). The single AHY Red Phalarope was initially captured at a

breeding site located 25.1 km west of Peard Bay (2) and was resighted 36 days later on the coast at the Peard Bay camp (B). Two of the HY Red Phalaropes captured at Barrow (C) moved southwest along the Chukchi coast to Peard Bay (B). These birds arrived at Peard Bay one and 11 days after last being detected at Barrow. Another HY Red Phalarope captured at Peard Bay (B) moved northeast to Barrow (C), arriving 12 days after its last detection at Peard Bay. A fourth HY Red Phalarope captured at the Colville Delta (E) also moved eastward to the Sagavanirktok Delta (F) in a single day.

We detected three of 41 Red-necked Phalaropes (7%; 1 AHY, 2 HY) after their initial capture. Red-necked Phalaropes moved both eastward and westward during the staging period (Fig. 3.2). The single AHY Red-necked Phalarope moved eastward from Prudhoe Bay (8) to the Canning Delta (G) and on to the Okpilak Delta (I), a total distance of 170.4 km. It was detected at the Canning Delta 24 days and the Okpilak Delta 25 days after being radio-marked at its nest site. Conversely, two HY Red-necked Phalaropes captured while staging at the Okpilak Delta (I) moved west across the Beaufort coast: one was detected at the Ikpikpuk Delta (D) and the other at the Canning Delta (G). These individuals were detected five and nine days after being last heard at the Okpilak Delta, respectively.

No Western Sandpipers were detected after leaving their capture site in either year of the study.

3.4.2. Residence time at capture sites

Our best model for post-capture residence time was one of constant survival and detection probability across all study species (Table 3.5); phalaropes were included (as a group) as a basis for comparison for the calidrid species. Using the best model, we estimated residence time for all species to be 6.5 days (95% C.I.: 3.4-9.6 days). Detection probability for all species (conditional upon survival) was 68% (95% CI: 58-78%). The second ranked model again contained a constant probability estimate but residence time estimates varied by species. The small change in $\Delta QAIC_c$ values (2.43 $QAIC_c$ units) between the best model and the second ranked model suggests that this model was also supported by the data. Based on the second ranked model, Semipalmated Sandpipers exhibited shorter post-capture residence times (4.3 days) than Western Sandpipers (7.9 days) and Dunlin (13.4 days; see Fig. 3.3 for 95% C.I.'s). We recognize that each individual was at a given location for some undetermined amount of time prior to when it was captured, thus residence time estimates in our study represent conservative estimates of how much time shorebirds spend at individual postbreeding sites after capture.

3.5 Discussion

3.5.1 Movement patterns reflect ultimate migration route

Our first prediction was supported by the majority of Semipalmated Sandpipers detected during this study; almost all moved eastward across the northern coast of Alaska after leaving their initial capture site. Also, the eight individuals that we detected multiple times all maintained an eastward direction of movement between detections. This matches our predicted direction of movement for this species, as the shortest distance from northern Alaska to either the Central Flyway or the east coast of Canada (the two alternate fall migration routes thought to be used by Alaskan-breeding Semipalmated Sandpipers; Harrington and Morrison 1979) would entail initially migrating east from Alaska. Many detected birds tended to track toward the Canning River, which we suspect might provide a southward migration corridor into the interior of Alaska from the northern coast (see below).

We initially predicted that because *arcticola* Dunlin migrate to Asia for the winter, we would see movements in a westerly direction across the ACP coast. However, we detected only 6 of 77 (7.8 %) radio-equipped Dunlin at sites away from their original capture site, so our data with which to test this prediction are limited, and the movement of these individuals may not be reflective of either ultimate migration routes or typical postbreeding movements for the species. The Dunlin we did detect moved both east and west across the study area. Andres (1989) also observed bi-directional movements of

Dunlin during his work at the Colville River Delta: 67% of Dunlin groups moved west, while 22% moved east. The east/west movements of Dunlin in both studies may be a function of the extended postbreeding period (average of 53 days for adults, based on our radio telemetry) exhibited by this species on the northern Alaska coast. It seems likely that individuals may have moved back and forth between postbreeding areas, depending on weather and intertidal conditions that may have influenced food availability and thus their ability to complete their flight and body feather molt while acquiring fat resources for southbound migration.

Also contrary to our first prediction, some individuals of the two phalarope species moved eastward along both the Chukchi and Beaufort Sea coasts. There are several potential explanations for why phalaropes may not always move west, our predicted direction of travel based on known migration routes. First, some Siberian Red Phalaropes are thought to join North American populations staging in the Beaufort Sea prior to fall migration (Alerstam and Gudmundsson 1999). Hatching-year Red Phalaropes captured in this study that subsequently moved eastward could have been Siberian birds migrating through the study area from the west. This is supported by a recent radar study of shorebird migration over the Arctic Ocean that recorded numerous observations of Red Phalaropes traveling from as far west as the Laptev Sea in Siberia to the Beaufort Sea (Alerstam et al. 2007). Alerstam and Gudmundsson (1999) proposed that Red Phalaropes may migrate eastward in the Beaufort Sea because their next southbound flight takes them overland across North America to the Pacific Ocean off the

coast of Mexico. Another explanation for eastward movement of phalaropes along the Chukchi Sea coast is that these individuals may have been heading north and east toward the permanent offshore ice edge in the Beaufort Sea (see images for Aug 2005 and 2006 at ftp://sidads.colorado.edu/DATASETS/NOAA/G02135/Aug for locations of ice edge during our study), where they have been previously observed into October (Johnson 1979, Johnson and Herter 1990). Phalarope migration patterns in relation to their use of the pack ice edge, along which their zooplankton prey concentrate, merits further investigation given recent decreases in ice extent across the Arctic Ocean (Stroeve et al. 2008).

3.5.2. Residence time and movements reflect migration strategy or timing of molt relative to migration?

We hypothesized that postbreeding behavior exhibited by a suite of calidridine sandpipers in northern Alaska should be related to either (a) migration strategy or the (b) timing of postnuptial molt relative to migration. We examined this question because Warnock (2010) suggested that the way birds migrated (hop, skip, or jump strategy) may be used to forecast whether birds exhibit staging or stopover behavior as well as site choice. Yet, other research supports the idea that timing of molt in relation to migration may also impact behavior and site choice of premigratory (postbreeding) Arctic birds (O'Hara et al. 2002, Bonier et al. 2007). Predictions for residence time and movement patterns for postbreeding shorebirds in northern Alaska as influenced by each strategy are

distinctly different. In this study, it appeared that timing of postnuptial molt relative to migration had more influence over these two aspects of shorebird behavior during the postbreeding period. We documented that Semipalmated Sandpipers, which as a species molt at wintering areas after fall migration, moved rapidly across the northern Alaska coast, often covering the approximately 100 km between detection locations in less than a day. Adults of this species were detected on the coast an average of only 16 days after capture at nest sites. Conversely, Dunlin, which undergo postnuptial molt during the breeding and postbreeding seasons, were detected on the coast an average of 53 days after capture at nest sites, and were not detected moving rapidly between sites along the coast (although our detection rate for this species was much lower than for Semipalmated Sandpipers). These species-specific differences are opposite of what we expected to see if migration strategies (short-hop vs. long-jump bouts of flight) were the most influential in determining postbreeding behavior. Under that scenario, we would expect that long-jump migrants like Semipalmated Sandpipers should need to stage for a prolonged period prior to leaving breeding areas for southbound migration, whereas shorter-hop migrants like Dunlin and Western Sandpipers, both of which likely migrate to other locations in Alaska prior to migration out of the Arctic, should exhibit shorter residence times at postbreeding sites and potentially use of multiple coastal sites with rapid flights in between.

We also found that residence times for Dunlin may be on average three times as long as for Semipalmated Sandpipers, and may border on the length typically thought of

as constituting "staging" at a given site (several weeks; Warnock 2010). Based on these species-specific differences in residence and movement timing, we suggest that Semipalmated Sandpipers are using coastal areas in northern Alaska as migratory stopover sites, whereas Dunlin may be using the same areas as premigratory staging sites. The results from examining our first hypothesis (showing that Semipalmated Sandpipers tended to move eastward in their ultimate migration direction, whereas other species did not) also support this distinction: Semipalmated Sandpipers' postbreeding movements are likely just initial migratory movements away from breeding areas. Western Sandpipers, which were hypothesized to show an intermediate set of behaviors given their molt strategy (postnuptial molt may begin in the Arctic, during, or after migration, and individuals may suspend molt during migration; Wilson 1994), were not detected after leaving their initial capture sites, but residence times at capture locations were intermediate to Semipalmated Sandpipers and Dunlin. Depending on the onset of postnuptial molt, some Western Sandpipers may actually "stage" at postbreeding sites, where as others may only stop over. The average of these behaviors in the population may create the intermediate residence time we observed for this species. Thus, the distinction between staging vs. stopover behavior within a species or even a larger interrelated group of species may be best viewed as a continuum rather than a clear dichotomy.

Hatching-year individuals of both species of phalaropes, which do not molt prior to migration, had short residence times and appeared to move relatively rapidly across the

coast of northern Alaska after being captured, although we did not have enough data for either species to examine whether migration strategy or migration timing was more likely affecting postbreeding movements. We were also unable to examine how long adult phalaropes spent at postbreeding areas compared to other species because we detected only one AHY bird of each species after being radio-equipped at nest sites.

3.5.3. Movement patterns away from the northern Alaska coast

Our telemetry data confirm that *arcticola* Dunlin, from as far east on the northern Alaska coast as the Colville River Delta, stage on the Yukon-Kuskokwim Delta after leaving the coast of northern Alaska. This movement pattern was previously hypothesized, given the direction of southbound migration for *arcticola* Dunlin and the presence of two morphometrically distinct groups of Dunlin staging on the YKD (Warnock and Gill 1996, R.E. Gill, *pers. comm.*). Our data also provide information on the relative length of time it takes for Dunlin to migrate to the YKD from northern Alaska: one HY Dunlin last detected on the Colville Delta on 16 August 2005 was detected on the YKD ten days later, on 26 August 2005. The remaining six Dunlin detected on the YKD showed larger intervals between being detected on the northern Alaska coast and the YKD, and all were detected later in the season, between 20 September and 4 October. We would expect the time individual Dunlin take to migrate between northern Alaska and the YKD to vary based on age, breeding location and success, molt schedule, fattening rate, food availability, and weather (Holmes 1971). Also, some *arcticola* individuals may bypass

the YKD entirely and migrate straight to Asia in the fall (Norton 1971); fat reserves and timing of departure from northern Alaska may dictate an individual's migration strategy. Alaska-banded *arcticola* Dunlin have been sighted in the fall in Sakhalin, Russia; whether these individuals had been staging on the YKD first before migrating to Russia remains unknown (Lanctot et al. 2009).

Flock (1973) surmised that radar observations of birds flying eastward past Distant Early Warning (DEW) stations on the northern Alaska coast were likely shorebirds heading east to the MacKenzie River Delta in western Canada, where they might fly south along the river corridor. Our data for Semipalmated Sandpipers suggest that all individuals of this species may not go as far east as the MacKenzie River before turning south: 65% of Semipalmated Sandpipers detected after initial capture in our study were found at the Canning River Delta or inland along the Canning River, and no individuals were detected moving east of the Canning River. One individual radio-marked at East Arey Lagoon near Barter Island was later detected at the Canning River Delta, having moved west (contrary to the predominant direction of Semipalmated Sandpiper movement) to reach the vicinity of the Canning River. It is possible that a large river corridor like the Canning could serve as a southward migration route for shorebirds, particularly since a riparian corridor may provide a low-elevation route across mountainous terrain such as that located to the south of Alaska's northern coast. Alternatively, the Canning River Delta may serve as a terminal staging site from which birds migrate east into Canada toward the Great Plains or Atlantic Provinces.

3.5.4. Data limitations

We caution that the limited number of birds detected at or away from their initial capture sites in our study means residence time estimates and movement patterns should be viewed as descriptive rather than quantitative. Each of our telemetry detections may represent only one of several movements made by each radio-equipped bird as they made their way from breeding sites to coastal postbreeding areas, or between different postbreeding sites. Individuals may have remained longer and used additional sites than we were able to record, and we could not determine the exact route of travel for most birds due to our limited telemetry coverage of the large study area (1000 km). Therefore, the movement patterns we observed in this study should be taken as conservative estimates of the timing and number of locations used by migrating shorebirds in northern Alaska. In addition, we have no way of knowing how long an individual was at a given site before we captured it, thus our estimates of residence time are likely conservative. The potential for underestimating residence time may be partially offset by a temporary effect of capture and radio-marking on how long birds stay at a given site. Previous studies found that radio-equipped Dunlin and Western Sandpipers stayed at capture sites longer than conspecifics that were already radio-marked when they arrived at the same site (Warnock and Bishop 1998, Warnock et al. 2004), although Skagen and Knopf (1994) found no relationship between handling time and length of stay for radio-equipped Semipalmated or White-rumped Sandpipers (*Calidris fuscicollis*).

These limitations, while important to note, should not fully negate the value of these data as a first attempt to provide insight into patterns of use of Alaska's northern coast by postbreeding shorebirds. Radio telemetry currently provides the only means by which to obtain data on movements of small shorebirds across a vast landscape such as northern Alaska. Band resighting methods would likely have resulted in a much lower detection probability (Plissner et al. 2000) and satellite transmitters are too large for any of the small- to medium-sized shorebird species we studied. The recent development of lightweight light-level geolocators may allow information on these species' movement patterns to be determined in the future (Clark et al. 2010), although the lack of daily light/dark cycles in the Arctic would have precluded the use of these devices until late in the postbreeding season. Also, these devices are still too large for species such as Semipalmated Sandpipers and Red-necked Phalaropes, and require that birds be recaptured for data retrieval.

Another factor limiting our data collection was the location of telemetry efforts in relation to shorebird migration routes. We were interested in use of coastal sites in northern Alaska by postbreeding shorebirds because these habitats may be impacted by oil and gas exploration and development in the near future (Bird et al. 2008). However, previous studies have suggested that shorebird migration may occur overland between the east and west portions of the Alaskan Arctic (e.g. Lehnhausen and Quinlan 1981, Gill et al. 1985), and researchers working inland of the coast have noted shorebirds moving through these habitats (R.E Gill, *pers. comm.,* A. Taylor, *unpubl. data*). It is possible that

some species of shorebirds may migrate inland when moving west across northern Alaska to shorten their flights, and perhaps gain quicker access to richer food resources found along the Chukchi and Bering Sea coasts. Our telemetry efforts were unable to detect individuals taking an inland route because all ARTS and field camps were immediately adjacent to the coast. Given our low detection rates for Dunlin, Western Sandpipers, and both phalarope species, we suspect this may be the case for at least some populations. On the other hand, previous landscape-scale surveys across the coast of northern Alaska documented large concentrations of postbreeding shorebirds using coastal habitats along the western Beaufort coast (Taylor et al. 2010), thus we are confident that not all shorebirds choose to take an inland route. A valuable follow-up study would be to conduct systematic aerial surveys or telemetry studies of inland areas of Arctic Alaska to assess shorebird use of these areas during the postbreeding period.

3.5.5. Monitoring and conservation implications

Despite the acknowledged limitations of our study and potential for a high degree of individual variation in shorebird movements prior to and during migration (as evidenced by satellite telemetry and light-level geolocator studies of larger shorebirds: Gill et al. 2009, Minton et al. 2010, Niles et al. 2010), we believe our results are indicative of relatively high spatial connectivity among northern Alaskan postbreeding areas for at least one shorebird species. Radio-equipped Semipalmated Sandpipers demonstrated a distinct pattern (eastward) in migratory route and postbreeding sites used as they began

their fall migration. Although we were unable to document this for Dunlin, the length of time between when adult Dunlin were captured on nest sites and when they were detected on the coast (~53 days) compared to the estimated residence time for this species at postbreeding areas (~14 days) indicates that this species may also use multiple coastal sites while staging, albeit not necessarily in the direction of their southbound migration nor where our telemetry efforts could detect them. These results have implications for monitoring population trends. For example, efforts to assess postbreeding shorebird abundance and distribution on the northern Alaska coast should take into account individuals' propensity to move between sites in order to minimize the possibility of double-counting or missing individuals across survey periods. Inaccurate population estimates could affect shorebird conservation and management measures in northern Alaska in terms of assessing magnitude of use at a given site, identifying and ranking postbreeding sites in order of importance, conducting biological assessments of impacts of development and climate change, and monitoring trends in shorebird populations through time. In particular, we advise that surveys for Semipalmated Sandpiper and phalarope abundance be conducted within the area of interest across as few days as possible, since individuals of these species have short residence times at a given site and are likely to migrate relatively long distances (100 km or more) between days. Also of note is the fact that two adult Dunlin radio-equipped on the same day at nearby nest sites in Barrow were detected together eight weeks later at Peard Bay. Whether these individuals traveled south from their breeding territories together remains unknown, but

the possibility of such group movement has implications for mark-recapture analyses that assume resightings or recaptures of individuals are independent events.

Another important implication of this study is that all coastal sites we studied were used by more than one species throughout the postbreeding period. Also, all detected individuals moved away from their initial capture locations while still remaining on the northern Alaska coast, and birds captured at nest sites did not appear to use only the coastal areas nearest their breeding sites. These results taken together suggest that Arctic-breeding shorebirds rely on multiple, dispersed sites to prepare for southbound migration, and that a concentration of shorebirds at a given location may represent individuals from a much wider range than the local tundra breeding area. Thus it is critical that managers consider the northern Alaska coast as a network of interconnected postbreeding sites serving multiple breeding populations of shorebirds. This knowledge has ramifications for Natural Resource Damage Assessment planning currently being undertaken in Alaska by the Coastal Response Research Center and the Oil Spill Recovery Institute to assess potential impacts from the accidental release of petroleum into the marine environment. The Minerals Management Service (MMS) estimated that 2.74 large crude oil spills (greater than 21 000 gallons) would occur in existing northern Alaska oilfields between 2004 and 2034 (MMS 2001). Although these spills may not occur in coastal habitats where shorebirds congregate, oil from such spills has the potential to reach coastal habitats via rivers that drain into the Arctic Ocean. Our data imply that such an event could impact birds from populations breeding across northern

Alaska because individuals from a large geographic area may group together at a single coastal site, and because other individuals may require resources from that site later in the postbreeding period to adequately prepare for migration. In sum, the cumulative population-level impact of an oil spill or other disturbance on postbreeding shorebirds is likely to be larger where spatial connectivity is high. This is of potential importance in developing mitigation strategies to address development in Arctic Alaska.

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3.7. Literature cited

Alerstam, T., and G.A. Gudmundsson. 1999. Migration patterns of tundra birds: tracking radar observations along the Northeast Passage. Arctic 52:346-371.

Alerstam, T., J. Backman, G.A. Gudmundsson, A. Hedenstrom, S.S. Henningsson, H. Karlsson. M. Rosen, and R. Strandberg. 2007. A polar system of intercontinental bird migration. Proceedings of the Royal Society B 274: 2523-2530.

Andres, B.A. 1989. Littoral zone use by post-breeding shorebirds on the Colville River Delta, Alaska. M.S. Thesis, The Ohio State University.

Bird, K.J., R.R. Charpentier, D. L. Gautier, D.W. Houseknecht, T.R. Klett, J.K. Pittman, T.W. Moore, C.J. Schenk, M.W. Tennyson, and C.J. Wandrey. 2008. Circum-arctic resource appraisal: estimates of undiscovered oil and gas north of the Arctic Circle. USGS Fact Sheet 2008-3049. Available online at http://pubs.usgs.gov/fs/2008/3049/.

Bonier, F., P.R. Martin,, J.P Jensen, L.K. Butler, M. Ramenofsky, and J.C. Wingfield. 2007. Pre-migratory life history staginges of juvenile Arctic birds: costs, constraints, and trade-offs. Ecology 88:2729-2735.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd Edition. Springer-Verlag, New York, New York, USA. 488 pp.

Butler, R.W., R.C. Ydenberg, and D.B. Lank. 2003. Wader migration on the changing predator landscape. Wader Study Group Bulletin 100: 130-133.

Clark, N. A., C. D. T. Minton, J. W. Fox, K. Gosbell, R.B. Lanctot, R. Porter, and S. Yezerinac. 2010. The use of geolocators to study wader movements. Wader Study Group Bulletin. 117: 173-178.

Connors, P.G. 1984. Ecology of shorebirds in the Alaskan Beaufort littoral zone. *In:* R. Barnes, D.M. Shell, and E. Ramirez, eds. The Alaskan Beaufort Sea: Ecosystems and environments. Academic Press, New York.

Connors, P.G., C.S. Connors and K.G. Smith. 1981. Shorebird littoral zone ecology of the Alaskan Beaufort coast. Final Report of Principal Investigators, Outer Continental Shelf Environment Assessment Program, National Oceanic and Atmospheric Administration 23:295– 396.

Fernández, G., J.B. Buchanan, R.E. Gill, Jr., R. Lanctot, and N. Warnock. 2008. Conservation Plan for Dunlin with Breeding Populations in North America (*Calidris alpina arcticola, C. a. pacifica, and C. a. hudsonia*), Version 1.0. Manomet Center for Conservation Sciences, Manomet, Massachusetts.

Flock, W.L. 1973. Radar observations of bird migration along the arctic coast of Alaska. Wilson Bulletin 85:259-275.

Gilders, M.A., and M.A. Cronin. 2000. North Slope oil field development. *In* Truett, J.C., and Johnson, S.R., eds. The natural history of an Arctic oil field. San Diego: Academic Press. 15–33.

Gill, R. E. 1996. Alaska shorebirds: status and conservation at a terminus of the East Asian-Australasian flyway. *In:* D. R. Wells and T. Mundkur, eds. Conservation of migratory waterbirds and their wetland habitats in the East Asian-Australasian flyway. Proceedings of an international workshop, Kushiro, Japan. Wetlands International-Asia Pacific, Kuala Lumpur, Publ. No. 116, and International Waterfowl and Wetlands Research Bureau, Tokyo.

Gill, R.E., C.H. Handel, and P.C. Connors. 1985. Bird utilization of Peard Bay and vicinity. *In:* P.J. Kinney, ed. Environmental characterization and biological utilization of Peard Bay. Anchorage: Bureau of Land Management/National Oceanic and Atmospheric Administration, Outer Continental Shelf Environmental Assessment Program. Final Reports of Principal Investigators 35:244-323.

Gill, R.E., T.L. Tibbitts, D.C. Douglas, C.M. Handel, D.M. Mulcahy, J.C. Gottschalk, N. Warnock, B.J. McCaffery, P.F. Battley, and T. Piersma. 2009. Extreme endurance flights by landbirds crossing the Pacific Ocean: ecological corridor rather than barrier? Proceedings of the Royal Society B 276:447-458.

Haig, S.M., and L.W. Oring. 1998. Wetland connectivity and waterbird conservation in the western Great Basin of the United States. Wader Study Group Bulletin 85:19-28.

Harrington B.A., and R.I.G. Morrison. 1979. Semipalmated Sandpiper migration in North America. Studies in Avian Biology 2:83-100.

Hicklin, P. and C.L. Gratto-Trevor. 2010. Semipalmated Sandpiper (*Calidris pusilla*). In: A. Poole, ed. The Birds of North America Online. Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/006

Holmes, R.T. 1971. Latitudinal differences in the breeding and molt schedules of Alaskan Red-backed Sandpipers (*Calidris alpina*). Condor 73:93-99.

Holmes, R.T. 1972. Ecological factors influencing the breeding season schedule of Western Sandpipers (*Calidris mauri*) in subarctic Alaska. American Midland Naturalist 87:472-491.

IPCC. 2001. Climate change 2001: The scientific basis. Contribution of Working Group I to the third assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Iverson, G.C. S.E. Warnock R.W. Butler, M.A. Bishoop, and N. Warnock. 1996. Spring migration of Western Sandpipers *(Calidris mauri)* along the Pacific coast of North America: a telemetry study. Condor 98:10-21.

Johnson, S.R. 1979. Avian ecology in Simpson Lagoon, Beaufort Sea, Alaska. *In:* Beaufort Sea Barrier Island-Lagoon Ecological Process Studies 1978. Annual Report, Research Unit 467, by LGL Limited-U.S., Inc. for the Outer Continental Shelf Environmental Assessment Program, National Oceanic and Atmospheric Administration, Boulder, CO.

Johnson, S.R., and D.R. Herter. 1989. The birds of the Beaufort Sea. BP Exploration (Alaska), Inc. Anchorage, AK.

Johnson, S.R., and D.R. Herter. 1990. Bird migration in the Arctic: a review. *In* E. Gwinner., ed. Bird migration: physiology and ecophysiology. Springer, Berlin, Germany.

Kaiser, A. 1995. Estimating turnover, movements, and capture parameters of resting passerines in standardized capture-recapture studies. Journal of Applied Statistics 22: 1039-1047.

Kovach Computing Services. 2005. Oriana Version 2.02c. Anglesey, Wales, U.K.

Lanctot, R.B., M. Barter, C. Chiang, R. Gill, M. Johnson, S. Haig, Z. Ma, P. Tomkovich, and M. Wunder. 2009. Use of band resightings, molecular markers and stable isotopes to understand the migratory connectivity of Dunlin breeding in Beringia and wintering in the East Asian-Australasian Flyway. Proceedings from the 2009 International Symposium on Coastal Wetlands and Water Birds Conservation, Chiku Research Center, Tainan, Republic of China (Taiwan), 1-3 December 2009.

Lank, D.B., R.W. Butler, J. Ireland, and R.C. Ydenberg. 2003. Effects of predation danger on migratory strategies of sandpipers. Oikos 103:303-319.

Lehnhausen, W.A., and S.E. Quinlan. 1981. Bird migration and habitat use at Icy Cape, Alaska. Anchorage: U.S. Fish and Wildlife Service, unpublished report.

Lindstrom, A., S. Daan, and G.H. Visser. 1994. The conflict between moult and migratory fat deposition: a photoperiodic experiment with bluethroats. Animal Behaviour 48:1173-1181.

Minton, C., K. Gosbell, P. Johns, M. Christie, J.W. Fox, and V. Afanasyev. 2010. Initial results from light level geolocator trials on Ruddy Turnstone *Arenaria interpres* reveal unexpected migration route. Wader Study Group Bulletin 117: 9–14.

MMS. 2001. Liberty Production and Development Plan, Final Environmental Impact Statement, Volume 1. OCS EIS/EA, MMS 2001-001, U.S. Department of the Interior, Minerals Management Service, Alaska OCS Region. Available online at http://www.mms.gov/alaska/ref/EIS%20EA/libertyfeis/Start_Here.pdf.

Naugle, D.E., K.F. Higgins, S.M. Nusser , and W.C. Johnson. 1999. Scale-dependent habitat use in three species of prairie wetland birds. Landscape Ecology 14:267-276.

Niles, L.J., J. Burger, R.R. Porter, A.D. Dey, C.D. T. Minton, P.M. Gonzalez, A.J. Baker, J.W. Fox, and C. Gordon. 2010. First results using light level geolocators to track Red Knots in the Western Hemisphere show rapid and long intercontinental flights and new details of migration pathways. Wader Study Group Bulletin 117:123-130.

Norton, D.W. 1971. Two Soviet recoveries of Dunlins banded at Point Barrow, Alaska. Auk 88:927.

O'Hara, P.D., D.B. Lank, and F.S. Delgado. 2002. Is the timing of moult altered by migration? Evidence from a comparison of age and residency classes of Western Sandpipers (*Calidris mauri*) in Panama. Ardea 90:61-70.

Piersma, T. 1987. Hop, skip, or jump? Constraints on migration of arctic waders by feeding, fattening, and flight speed. Limosa 60: 185-194 (in Dutch).

Plissner, J.H., S.M. Haig, and L.W. Oring. 2000. Postbreeding movements of American Avocets and implications for wetland connectivity in the western Great Basin. Auk 117:290-298.

Prater, A.J., J.H. Marchant, and J. Vuorinen. 1977. Guide to the identification and aging of holarctic waders. Field Guide No. 17, British Trust for Ornithology, Tring, U.K.

Rubega, M.A., D. Schamel, and D.M. Tracy. 2000. Red-necked Phalarope (*Phalaropus lobatus*). *In* A. Poole and F. Gill, eds. The Birds of North America, No. 538. The Birds of North America, Inc., Philadelphia, PA.

Sanzenbacher, P.M., S.M. Haig, and L.W. Oring. 2000. Application of a modified harness design for attachment of radio transmitters to shorebirds. Wader Study Group Bulletin 91:16-20.

Skagen, SK., and F.L. Knopf. 1994. Residency patterns of migrating sandpipers at a midcontinental stopover. Condor 96:949-958.

Stroeve, J., M. Serreze, S. Drobot, S. Gearheard, M. Holland, J. Maslanik, W. Meier, and T. Scambos. 2008. Arctic sea ice extent plummets in 2007. *EOS* Transactions of the American Geophysical Union 89:13–14.

Taylor, A.R., R.B.Lanctot, A.N. Powell, F. Huettmann, D.A. Nigro, and S.J. Kendall. 2010. Distribution and community characteristics of staging shorebirds on the northern coast of Alaska. Arctic 63:461-467.

Tracy, D.M., D. Schamel, and J. Dale. 2002. Red Phalarope (*Phalaropus fulicarius*). *In* A. Poole and F. Gill, eds. The Birds of North America, No. 698. The Birds of North America, Inc., Philadelphia, PA.

Warnock, N. 2010. Stopping versus staging: the difference between a hop and a jump. Journal of Avian Biology 41:621-626.

Warnock, N., and M.A. Bishop. 1998. Spring stopover ecology of migrant Western Sandpipers. Condor 100:456-467.

Warnock, N..D., and R.E. Gill. 1996. Dunlin (*Calidris alpina*). *In* A. Poole and F. Gill, eds. The Birds of North America, No. 203. The Birds of North America, Inc., Philadelphia, PA.

Warnock, N., J.Y. Takekawa, and M.A. Bishop. 2004. Migration and stopover strategies of individual Dunlin along the Pacific coast of North America. Canadian Journal of Zoology 82:1687-1697.

Warnock, N., and S. Warnock. 1993. Attachment of radio-transmitters to sandpiper: review and methods. Wader Study Group Bulletin 70:28-30.

Watson, G. E., and G. J. Divoky. 1974. Pelagic bird and mammal observations in the western Beaufort Sea, late summer 1971 and 1972. U.S. Coast Guard Oceanogra. Rep. CG-373.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46 Supplement:120-138.

Wilson, W.H. 1994. Western Sandpiper (*Calidris mauri*). *In* A. Poole and F. Gill, eds. The Birds of North America, No. 90. The Birds of North America, Inc., Philadelphia, PA.

World Wildlife Fund/Audubon Alaska. 2007. Comments to Minerals Management Service on Draft Environmental Impact Statement for the Proposed Final Program, Outer Continental Shelf Oil and Gas Leasing Program, 2007-2012. Submitted 22 November 2007, Anchorage, AK.

Ydenberg, R.C., R.W. Butler, and D.B. Lank. 2007. Effects of predator landscapes on the evolutionary ecology of routing, timing, and molt by long-distance migrants. Journal of Avian Biology 38:523-529.

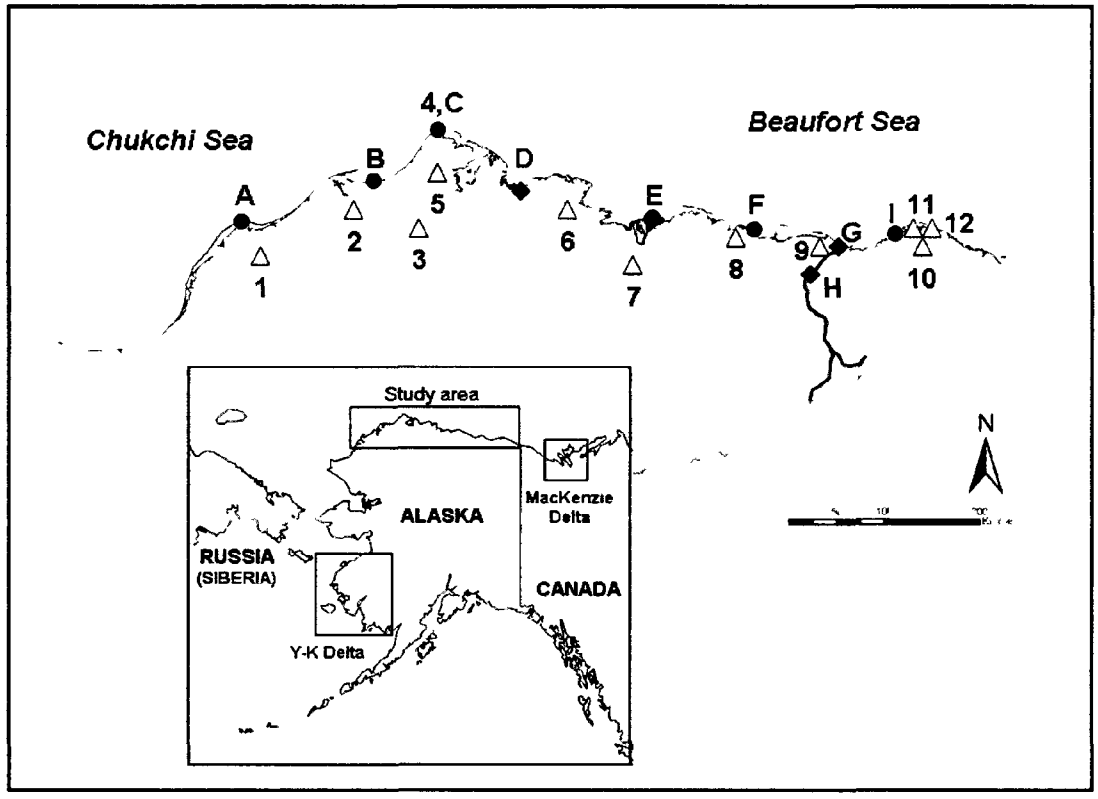
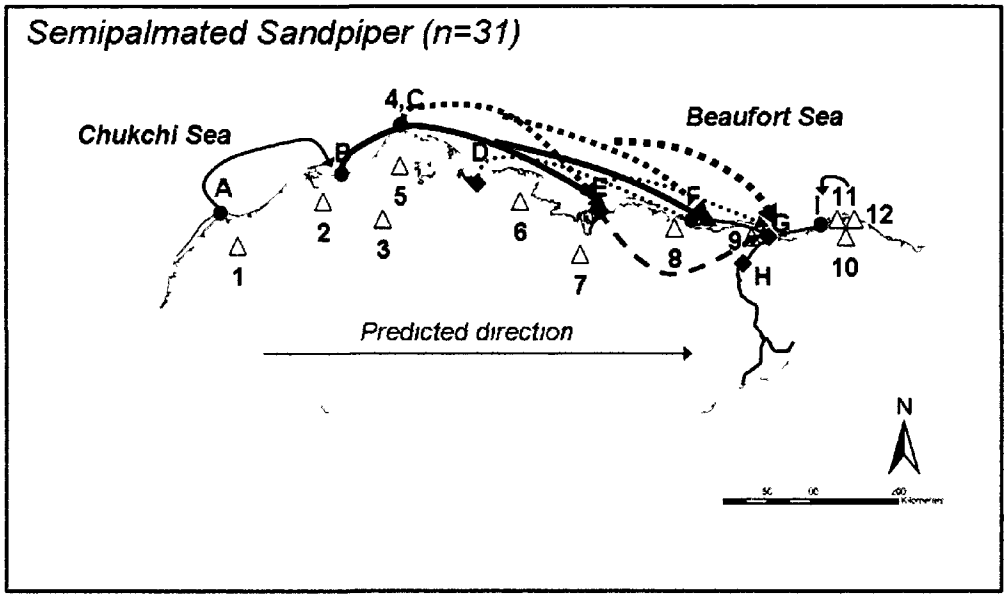
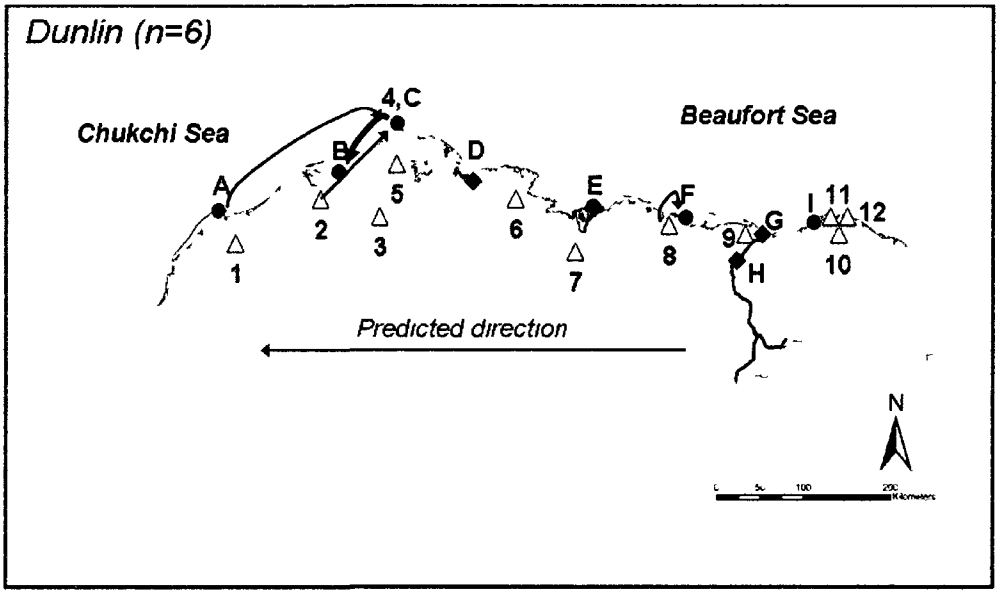
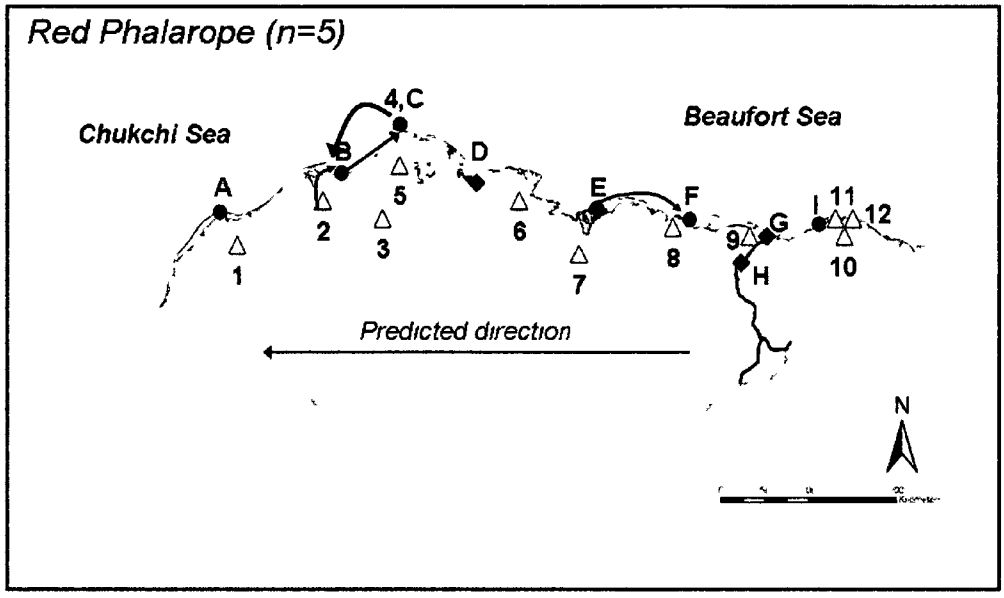


Figure 3.1. Location of transmitter deployment and detection sites on the northern Alaska coast 2005-2007. Unfilled triangles represent sites where birds were captured during breeding. Filled circles indicate the site was a staffed field camp in at least one year of the study. Filled diamonds represent unmanned telemetry sites in at least one year of the study. Table 3.1 gives dates and activities done at each site. The outline of the Canning River within the study area is shown in bold; locations G and H represent telemetry stations at the delta and along the river, respectively.


Semipalmated Sandpiper (n=31)
Chukchi Sea
Beaufort Sea
4,C
B
D
A
E
F
G
I
11
12
5
2
3
6
9
8
H
10
1
7
Predicted direction
N


Dunlin (n=6)
Chukchi Sea
Beaufort Sea
4,C
B
D
A
E
F
G
I
11
12
5
2
3
6
9
8
H
10
1
7
Predicted direction
N


Red Phalarope (n=5)
Chukchi Sea
Beaufort Sea
4,C
B
D
A
5
E
F
I
11
12
2
3
6
G
9
1
8
H
10
7
Predicted direction
N

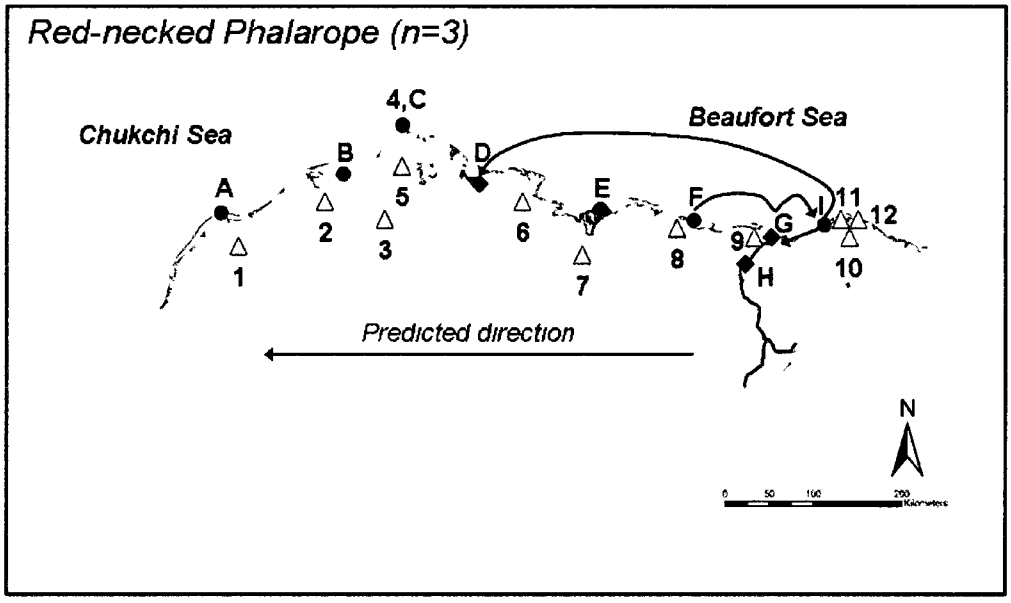

Red-necked Phalarope (n=3)
Chukchi Sea
Beaufort Sea
4,C
B
D
A
5
E
F
I
11
12
2
6
3
G
9
8
1
H
10
7
Predicted direction
N

Figure 3.2. Movement patterns of four species of shorebirds subsequently detected at a new location. Shorebirds were equipped with radio transmitters at one site and detected moving to another site. Thickness of lines represent the number of birds showing a particular movement pattern, with the thinnest lines representing one individual and the thickest lines representing three individuals. Different line patterns were used in congested portions of the map for Semipalmated Sandpipers to differentiate patterns more easily. Predicted direction of movement for each species is indicated.

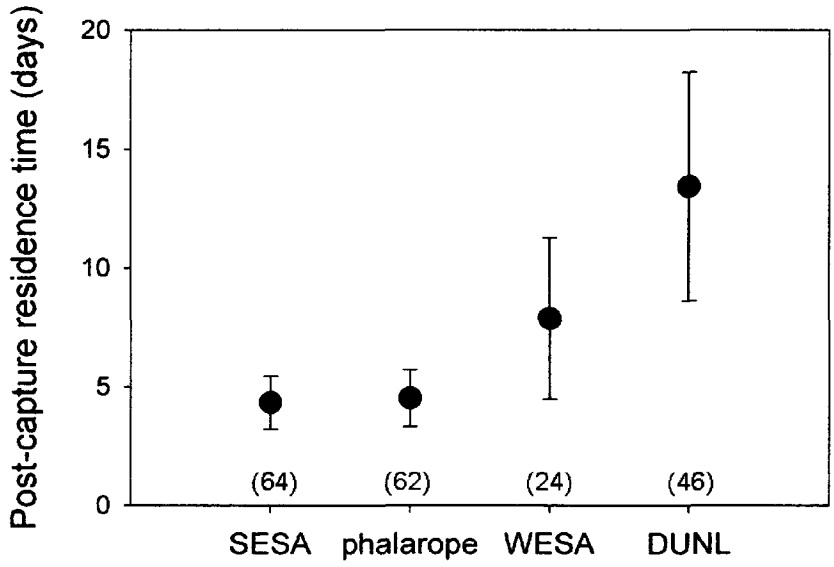


Figure 3.3. Post-capture residence time for radio-equipped shorebirds captured at postbreeding sites on the northern coast of Alaska. See Table 3.1. and Figure 3.1. for capture locations. SESA = Semipalmated Sandpiper, phalarope = both Red and Red-necked Phalaropes combined, WESA = Western Sandpiper, DUNL = Dunlin. Sample sizes are given in parentheses above each species' abbreviation.

Table 3.1. Locations, dates, and types of field activity associated with radio-equipping and monitoring shorebirds on Alaska's northern coast. Breeding locations represent the centers of polygons within which a sample of birds was captured at dispersed nest sites; postbreeding locations are more precise because they represent fixed-site camps or ARTS. For activity types, D = deployment, ARTS = automated remote telemetry station, MT = manual telemetry searches at field camps, and n/a = non-applicable. See Fig. 3.1 for map locations.

Season and				Dates of Activity			Activity		
Map Location	Location	Lat	Long	2005	2006	2007	2005	2006	2007
Breeding									
1	NPRA-W	70.5°N	160.4°W	n/a	6/24	n/a	n/a	D	n/a
2	NPRA-NW	70.6°N	158.3°W	n/a	6/19-6/23	n/a	n/a	D	n/a
3	Meade River	70.5°N	157.7°W	7/1-7/3	n/a	n/a	D	n/a	n/a
4	Barrow tundra	71.3°N	156.6°W	6/27-7/1	6/30-7/9	6/23-6/25	D	D	D
5	NPRA-NE	71.0°N	156.3°W	n/a	6/19-6/22	n/a	n/a	D	n/a
6	Teshekpuk Lake	70.4°N	153.1°W	6/27-6/29	n/a	n/a	D	n/a	n/a
7	NPRA-E	70.8°N	154.0°W	n/a	6/19-6/23	n/a	n/a	D	n/a
8	Prudhoe tundra	70.2°N	148.1°W	7/9-7/10	6/27-7/4	n/a	D	D	n/a
9	Canning tundra	70.1°N	145.9°W	7/1-7/6	6/26-7/9	7/2-7/12	n/a	D	D
10	Jago-Bitty River	69.7°N	143.7°W	n/a	6/29-6/30	n/a	n/a	D	n/a
11	E Arey Lagoon	70.1°N	143.7°W	n/a	7/2-7/5	n/a	n/a	D	n/a
12	Jago Delta tundra	70.1°N	143.2°W	n/a	7/3-7/4	n/a	n/a	D	n/a

Table 3.1 continued.

Postbreeding

A	Kasegaluk	70.301°N	161.888°W	8/1-8/25
B	Peard Bay	70.812°N	158.323°W	7/26-8/25
C	Barrow	71.336°N	156.597°W	7/25-8/29
D	Ikpikpuk Delta	70.793°N	154.299°W	7/30-8/25
E	Colville Delta	70.473°N	150.564°W	8/1-8/22
F	Sagavanirktok	70.251°N	147.807°W	7/29-8/23
G	Canning Delta	70.145°N	145.866°W	6/26-8/22
H	Canning River	69.863°N	146.413°W	n/a

7/24-9/2	n/a	ARTS	D, ARTS MT	n/a
7/13-9/2	n/a	D ARTS MT	D ARTS MT	n/a
7/15-9/9	n/a	D ARTS MT	D MT	n/a
n/a	n/a	ARTS	n/a	n/a
7/19-8/30	n/a	D ARTS MT	D ARTS MT	n/a
7/24-9/7	n/a	D ARTS MT	D	n/a
6/29-9/2	7/19-7/30	ARTS	ARTS	D ARTS MT
6/28-9/7	7/16-7/24	n/a	ARTS	ARTS

Table 3.1 continued.

I	Okpilak Delta	70.080°N	144.001°W	8/8-8/24

7/16-7/24	n/a	D ARTS MT	D ARTS MT	n/a

Table 3.2. Radio transmitter breakdown: transmitters deployed by season, location, species, year, and age group of on shorebirds on Alaska's northern coast. SESA = Semipalmated Sandpiper, DUNL = Dunlin, REPH = Red Phalarope, RNPH = Red-necked Phalarope, WESA = Western Sandpiper.

			2005		2006		2007	
Season	Location	Species	HY	AHY	HY	AHY	HY	AHY
Breeding	Barrow tundra	SESA	0	3	0	5	0	10
		DUNL	0	8	0	5	0	0
		REPH	0	5	0	5	0	0
	NPR-A[1]	SESA	0	7	0	10	0	0
		DUNL	0	6	0	10	0	0
		REPH	0	10	0	10	0	0
	Prudhoe tundra	SESA	0	3	0	5	0	0
		DUNL	0	0	0	5	0	0
		REPH	0	0	0	4	0	0
	Canning tundra	SESA	0	4	0	3	0	14
		DUNL	0	0	0	4	0	0
		REPH	0	3	0	0	0	0
		RNPH	0	0	0	2	0	0
	Arctic Refuge[2]	SESA	0	0	0	7	0	0
		RNPH	0	0	0	5	0	0
	Total breeding		0	49	0	80	0	24
Postbreeding	Kasegaluk	SESA	0	0	4	1	0	0
		DUNL	0	0	3	3	0	0
		REPH	0	0	4	0	0	0
		RNPH	0	0	0	1	0	0
		WESA	0	0	4	0	0	0
	Peard Bay	SESA	5	0	5	0	0	0
		DUNL	3	0	0	0	0	0
		REPH	6	0	5	0	0	0
		RNPH	0	0	3	0	0	0
		WESA	0	0	3	0	0	0

Table 3.2 continued.

Barrow	SESA	5	0	5	0	0	0
	DUNL	3	0	11	0	0	0
	REPH	6	0	5	0	0	0
	RNPH	0	0	1	0	0	0
	WESA	5	0	4	0	0	0
Colville Delta	SESA	4	1	3	2	0	0
	DUNL	4	0	6	0	0	0
	REPH	3	0	3	0	0	0
	RNPH	3	0	2	1	0	0
Sagavanirktok	SESA	4	0	5	0	0	0
	DUNL	0	0	5	1	0	0
	RNPH	4	0	3	0	0	0
Canning Delta	SESA	0	0	0	0	14	1
Okpilak Delta	SESA	7	0	10	1	0	0
	RNPH	5	0	5	0	0	0
	WESA	1	0	0	0	0	0
Total postbreeding		68	1	99	10	14	1

[1]NPR-A locations include Teshekpuk Lake, Meade River, NPRA-W, NPRA-NW, NPRA-NE, and NPRA-E sites from Table 3 1 These sites were accessed by helicopter during a breeding season avian influenza study in 2005-2006, allowing only a small number of radio transmitters to be deployed at any one area

[2]Arctic Refuge locations include Jago-Bitty River, East Arey Lagoon, and Jago Delta tundra sites from Table 3 1 These locations were also accessed opportunistically during a single field trip in 2006 and thus only a small number of transmitters were deployed at each site

Table 3.3. Locations and lengths of time between detections of eight radio-equipped Semipalmated Sandpipers. Individuals were captured at coastal postbreeding sites and heard multiple times along the ACP coastline in 2005 and 2006. "Radio Date/Last Heard" column refers to when the individual was captured and radio-equipped, followed by the last date that individual was detected at its capture location. Date for both events was the same if only one date given in this column. "Subsequent Detection Location" "Detection Date," and "Distance" columns refers to where, when and how far a bird moved as it traveled to subsequent locations. For the first line of data for a given individual, "Distance" refers to the distance between the initial capture site and this new detection location. For each subsequent line of data for a given individual, "Distance" refers to how far it traveled from its prior location (i.e., not its initial capture site). See Figure 1 for locations.

Individual	Age	Capture Location	Radio Date/ Last Heard	Subsequent Detection Location	Detection Date	Distance (km)
1	AHY	Kasegaluk	4-Aug-06	W of Peard Bay	9-Aug-06	128.23
				Peard Bay	14-Aug-06	14.75
2	HY	Peard Bay	1-Aug-05	Colville Delta	8-Aug-05	290.74
				Sagavanirktok	8-9 Aug 05	90.41
				Canning Delta	10-Aug-05	89.11
3	HY	Peard Bay	28-Jul-06/	Colville Delta	6-7Aug 06	285.43
			2-Aug-06	Sagavanirktok	7-Aug-06	105.22

Table 3.3 continued.

4	HY	Barrow	30-Jul-05/	Colville Delta	4-Aug-05	241.14
			5-Aug-05	Sagavanirktok	5-Aug-05	88.40
				Canning Delta	5-Aug-05	86.87
5	HY	Barrow	4-Aug-05/	Sagavanirktok	7-Aug-05	330.52
			7-Aug-05	Canning Delta	7-Aug-05	86.95
6	HY	Barrow	28-Jul-06/	Sagavanirktok	6-Aug-06	343.35
			31-Jul-06	Canning River	9-Aug-06	67.87
7	HY	Barrow	31-Jul-06/	Colville Delta	8-Aug-06	241.09
			7-Aug-06	Canning River	9-Aug-06	170.22
8	HY	Colville Delta	1-Aug-05	Sagavanirktok	4-Aug-05	89.09
				Canning Delta	5-Aug-05	89.18

Table 3.4. Data for radio-equipped Dunlin captured on the ACP and later heard on the Yukon-Kuskokwim Delta (YKD) during aerial surveys in 2005. "Capture Location" refers to where on the ACP the birds were originally equipped with radio transmitters. Under the overall Date column, "Capture Date" refers to date of initial capture, "Last on ACP" refers to the date when the bird was last known to be on the ACP, and "Detection YKD" are dates when each individual was detected on the YKD.

			Date		
Individual	Age	Capture Location	Capture	Last on ACP	Detection on YKD
1	AHY	Barrow	1-Jul-05	1-Aug-05	4 & 7 Oct
2	AHY	Barrow	29-Jun-05	3-Jul-05	4 & 7 Oct
3	AHY	Teshekpuk Lake	29-Jun-05	30-Jun-05	20 Sep
4	AHY	Meade River	2-Jul-05	3-Jul-05	20 Sep; 4 & 7 Oct
5	HY	Barrow	4-Aug-05	29-Aug-05	20 Sep
6	HY	Colville Delta	3-Aug-05	16-Aug-05	26 Aug; 20 Sep
7	HY	Colville Delta	5-Aug-05	20-Aug-05	30 Sep

Table 3.5. Model selection results for Cormack-Jolly-Seber survival analysis to estimate residence time. Analysis was done on shorebirds detected multiple times at their site of capture. $QAIC_c$ (Akaike's Information Criterion adjusted for small sample sizes and lack of model fit) was used as our model selection criterion. For each model, $\Delta QAIC_c$ = the change in $QAIC_c$ units between the top model and the model of interest; $QAIC_c$ weight (w_i) = a measure of the relative support in the data for each model; likelihood = the evidence ratio for each model, and K = the number of parameters. Minimum $QAIC_c$ = 202.76.

Model	K	$\Delta QAIC_c$	w_i	Likelihood
1 Φ(.), p(.)	2	0.00	0.6154	1.0000
2 Φ(4 species), p(.)	5	2.43	0.1827	0.2970
3 Φ(4 species* linear trend), p(.)	6	4.25	0.0734	0.1192
4 Φ(5 species), p(.)	6	4.28	0.0724	0.1177
5 Φ(4 species*quadratic trend), p(.)	7	6.25	0.0271	0.0440
6 Φ(5 species*capture date), p(.)	7	6.30	0.0263	0.0428
7 Φ(5 species), p(5 species)	10	11.42	0.0020	0.0033
8 Φ(5 species*capture date), p(5 species)	11	13.46	0.0007	0.0012

4. COMPARATIVE MACROPHYSIOLOGY: EVALUATING SITE QUALITY IN THE CONTEXT OF AVIAN LIFE HISTORY STRATEGIES[1]

4.1. Abstract

Variation in physiologic metrics may indicate differences in site function or quality for migratory shorebirds. This has advantages for understanding large-scale patterns of abundance or distribution, and for conservation or management of important habitats. However, it is important to take into account species-specific differences in life history strategies when comparing patterns of site quality across species. We sought to use comparative physiology on a population level to examine macrophysiological questions regarding foraging site function and quality for postbreeding shorebirds on the northern Alaska coast. Specifically, we used plasma triglyceride and corticosterone levels from individuals of three species with varying prebasic molt strategies to test a suite of hypotheses, and to assess whether physiological metrics could be a useful proxy for site quality across species. Species-specific patterns of molt intensity and capture dates confirmed that Dunlin exhibited a "molt-then-migrate" strategy while Semipalmated Sandpipers exhibited a "migrate-then-molt" strategy. Western Sandpipers were intermediate between these two species in molt strategy. Postbreeding sites in northern Alaska may function as stopover/resting sites for Semipalmated Sandpipers and some Western Sandpipers, whereas they may function as staging/molting sites for Dunlin and

[1] Formatted for submission to *Auk* as Taylor, A.R., R.B. Lanctot, T.D. Williams, A S Kitaysky, and A.N. Powell Comparrative landscape physiology: evaluating site quality in the context of avian life history strategies

other Western Sandpipers. Molt intensity had a larger influence on triglyceride levels for Dunlin compared to the other species. Sites differed in quality as assessed by both metrics, although the ranking of sites as high or low quality was not consistent across all species and metrics. We used mean linear density of each species at each site as an independent measure of site quality, and examined correlations between density and mean site-specific triglyceride and corticosterone values. Corticosterone was positively correlated with density for Semipalmated Sandpipers only; triglyceride was not significantly correlated with density for any species. High densities of birds may result in depletion of food resources, leading to lower fueling rates and therefore lower triglyceride levels; or, linear density may be a poor indicator of site quality from a shorebird perspective. We suggest that physiological tools for assessing site quality in migratory birds should utilize multiple metrics, and should take into account differences in life history strategies and resulting behavior patterns if making inferences from multiple species.

4.2. Introduction

For birds undertaking long-distance migration, the ability to accumulate fuel reserves prior to and during migration is a primary factor determining migration performance (Alerstam and Lindstrom 1990, Schaub and Jenni 2001), and therefore is likely to affect individuals' choice of staging or stopover sites as well as timing of use of these sites.

Assessments of how important such sites are to migratory birds have often based on observations of abundance, stopover length, or mass gain between recaptures (Hutto 1985, Winker et al. 1992, Holmgren et al. 1993a), but species-specific life history strategies (such as the timing of prebasic molt in relation to migration) likely influence these metrics and are not always investigated.

Systematic aerial and ground surveys along the coast of northern Alaska (which lies adjacent to the Arctic Coastal Plain, an important breeding area for shorebirds) indicate that shorebirds move from tundra breeding areas to coastal postbreeding sites prior to fall migration; that shorebird use of coastal habitats during this period is non-uniform; and that postbreeding "hotspots," or areas of concentrated abundance, appear to be persistent through time (Connors 1984, Taylor et al. 2010). While assessments of density or abundance help us determine which sites are used by postbreeding shorebirds, they do not enable us to understand the mechanisms behind the observed distribution patterns (Taylor et al. 2007).

4.2.1. Effect of prebasic molt strategy on postbreeding shorebird behavior

Scheduling important life history events such as molt and migration likely forms the basis for evolution of many avian life history strategies, because selection favors temporal separation of these energetically intensive events (Payne 1972, O'Hara et al. 2002). We studied three Arctic-breeding shorebird species that are representative of different prebasic molt strategies. Semipalmated Sandpiper (*Calidris pusilla*) adults typically molt

at wintering areas after fall migration; juveniles undergo a partial to almost complete postjuvenal molt of body and flight feathers that is usually completed at wintering areas (Holmes 1972, Prater et al. 1977, Hicklin and Gratto-Trevor 2010). Adult Dunlin *(C. alpina arcticola* – the northern Alaska subspecies) molt flight and body feathers at breeding and postbreeding sites prior to fall migration. Juveniles start post-juvenal body feather molt in the Arctic before juvenal molt is fully complete, but may finish body molt at wintering areas (Holmes 1966, Holmes 1971, Warnock and Gill 1996). Western Sandpipers (*C. mauri*) exhibit an intermediate molt strategy with some individuals starting body feather molt in the Arctic prior to fall migration whereas others molt at wintering areas (Wilson 1994). Juveniles undergo a partial body feather molt in the fall, but retain substantial juvenal plumage until either spring or the following fall (Cramp and Simmons 1983, Wilson 1994). Adult Western Sandpipers may suspend body molt during migration if molt is started in the Arctic (Wilson 1994), but it is unknown whether juvenile Western Sandpipers do this as well. Several previous studies have documented that differences in flight feather molt strategies in this species may be related to overall migration distance (Nebel et al. 2002, O'Hara et al. 2005); it is not known whether migration distance also influences timing of body molt.

A radio telemetry study of these three species on the coast of northern Alaska established that postbreeding site use differs among species (Chapter 3 of this dissertation). Juvenile Semipalmated Sandpipers remained at their capture sites for only a few days and moved rapidly between sites, while juvenile Dunlin remained at their

capture sites for almost two weeks and were not detected moving between sites. Juvenile Western Sandpipers remained at capture sites for approximately a week and were also not detected moving between sites. Thus, Semipalmated Sandpipers were using postbreeding sites only briefly, possibly just to rest between migratory flights, whereas Dunlin were likely using sites to complete molt and prepare for migration (Chapter 3). Western Sandpipers appeared to show individually variable behavior and site use depending on whether they had initiated body molt. Differences in species-specific strategies are further highlighted by Connors (1984), who determined that pre-migratory fat deposition changed with date across these three species at coastal sites in Barrow. Dunlin showed a significant increase in fat scores with date and remained late into the season at postbreeding sites, whereas Semipalmated Sandpipers left the Arctic sooner and had only moderate fat scores throughout the season. How molt strategy affects the behavior of postbreeding shorebirds could be considered to be a continuum based on individual life history characteristics. At the extremes of this continuum are individuals that migrate south, then molt at wintering areas; such individuals would be predicted to have shorter stays in the Arctic overall and at each postbreeding site specifically. In contrast, individuals that molt during or prior to fall migration are predicted to have longer stays in the Arctic overall and at each postbreeding site.

4.2.2. Physiological assessment of site quality

Increasingly it is recognized that landscape-scale ecological patterns may be created by underlying physiological mechanisms acting on individual organisms (macrophysiology; e.g. Chown et al. 2004, Homyack 2010). Numerous researchers have used a wide range of physiologically-based techniques to examine differential habitat quality at wintering areas (e.g., Marra and Holberton 1998) and at stopover sites (e.g., Guglielmo et al. 2005, Acevedo Seaman et al. 2006). We sought to use comparative physiology on a population level to test macrophysiological predictions of foraging site function and quality for postbreeding shorebirds on the northern Alaska coast. Specifically, we used plasma triglyceride and corticosterone levels to examine predictions for how species with different prebasic molt strategies use postbreeding foraging sites, and to test whether site quality varied across the range of sites we studied.

Shorebirds preparing for migration undergo periods of hyperphagia that facilitate the storage of adequate lipid reserves for fueling long distance flight (Berthold 1975, Stevens 1996). Byproducts of cellular lipid metabolism can be used to predict the physiological state of migratory birds with respect to the rate of mass gain or loss (Ramenofsky 1990, Jenni-Eiermann and Jenni 1996, Williams et al. 1999). Triglycerides, which appear in the bloodstream as a result of dietary lipid ingestion, have been shown to be the best measure of fuel deposition rate in free-living Western Sandpipers, with higher plasma triglyceride levels indicating higher fueling rates in individual free-living birds (Guglielmo et al. 2002, Williams et al. 2007). Further study

has shown that population-level triglyceride levels may be used to infer site quality across a series of migratory stopovers: triglyceride levels were higher at sites where macrofaunal prey density was higher (Acevedo Seaman et al. 2006) or refueling rates were greater (Guglielmo et al. 2005).

Corticosterone is the steroid hormone produced by birds to facilitate life history changes, such as the transition from breeding to postbreeding condition (Lohmus et al. 2003) or from pre-migratory fattening to migratory flight (Piersma et al. 2000). For migratory birds in general, increases in baseline circulating corticosterone levels prior to migration may stimulate foraging activity and lipogenesis, thus facilitating the storage of lipids as fuel for long-distance flight (reviewed by Holberton et al. 1996). Baseline corticosterone increased during staging in Bar-tailed Godwits (*Limosa lapponica*; Landys-Cianelli et al. 2002), and peaked just prior to what would have been the initiation of migratory flight in captive Red Knots (*Calidris canutus*; Piersma et al. 2000). On a population level, one could expect that high quality sites might enable individuals to adequately prepare for and depart on migratory flights more rapidly than at lower quality sites, thus mean corticosterone levels for captured individuals should be higher at these sites.

The timing of prebasic molt in relation to fall migration should affect hormonal and metabolic profiles because such life history events are thought to be mediated by physiological mechanisms (Cherel et al. 1988, Totzke and Barlein 1998, Jenni-Eiermann et al. 2002, O'Reilly and Wingfield 2003), thus physiological metrics indexing site

quality should be considered in the context of species-specific molt strategies. Captive Red Knots showed significantly lower triglyceride levels (indicating slowed lipid storage) during body molt, and those levels decreased with increasing molt intensity (Jenni-Eiermann et al. 2002). Canada Geese *(Branta canadensis)* breeding in northern Manitoba showed the lowest triglyceride levels of the year during molt prior to fall migration (Mori and George 1978). Although no studies have examined the relationship between molt and corticosterone levels in pre-migratory shorebirds, baseline corticosterone levels were lower in migratory passerine species undergoing prebasic molt (Jenni-Eiermann and Jenni 1996). This downregulation of baseline corticosterone levels may be to allow protein deposition necessary for feather growth and/or to prevent chronic exposure to deleteriously high corticosterone levels (Romero 2002, Romero et al. 2005).

4.2.3. Study hypotheses

To test the efficacy of using physiological metrics to assess site quality for migratory birds with varying molt strategies, we considered a number of hypotheses for how population-level values of triglyceride, corticosterone, and density should differ among strategies and across sites of varying quality (Fig. 4.1). We developed these hypotheses under two scenarios of molt strategy and two levels of site quality, which likely represent extreme cases, but provide a framework for understanding the relationship between these variables. First, we wanted to confirm the connection between molt strategy and behavior patterns seen in Chapter 3. We expected that individuals with a molt-then-

migrate strategy (e.g., most Dunlin) should show a higher mean molt intensity across the population (although the mean is likely to decline with time as most individuals complete molt) than individuals with a migrate-then-molt strategy (e.g. most Semipalmated Sandpipers). Given that molt strategy mediates behavior via physiology, we hypothesized that triglyceride and corticosterone levels should be lower in actively molting individuals. An individual's triglyceride and corticosterone levels may also depend on the date it is captured, regardless of its molt strategy, simply because a bird captured later in the year is likely to be closer to the start of migration when corticosterone (reflecting migratory readiness) is thought to peak (Piersma et al. 2000, Landys-Cianelli et al. 2002). Triglyceride levels may also change just before the onset of flight if fueling rates taper off or increase just prior to flight. Individuals with a molt-then-migrate strategy (most Dunlin) are more likely to be captured later in the season, and therefore capture date should have a greater influence on physiological metrics compared to birds with a migrate-then-molt strategy (most Semipalmated Sandpipers), because migratory readiness in the former will change more dramatically through time. If this prediction holds true, capture date should be considered as a covariate in multi-species analyses of site quality as assessed by physiology. Because individual Western Sandpipers may exhibit either molt strategy, we hypothesized that their population level response would be intermediate to that of Dunlin or Semipalmated Sandpipers.

Secondly, we investigated how site quality influenced triglyceride and corticosterone levels through time within each molt strategy (Fig. 4.1). Because pre-

migratory shorebirds likely operate under a time-minimizing migration model (Alerstam and Lindstrom 1990, Lindstrom et al. 2002), individuals should select for sites that allow high fuel deposition rates, enabling them to reach departure fat loads sooner and thus begin migration earlier. High quality sites should thus be evidenced by higher triglyceride levels and higher corticosterone levels (indicating migratory preparedness), but this is likely to vary by molt strategy. For birds employing a migrate-then-molt strategy (most Semipalmated Sandpipers), we hypothesized there would be less effect of site quality on triglyceride levels, because these individuals are likely using sites only briefly and thus their metabolic profiles may integrate fueling rate information over several sites. Conversely, we expected a larger effect of site quality for birds employing a molt-then-migrate strategy (most Dunlin) because these individuals are using sites for long enough that differences in fueling rates are evident and likely reflect site choice. The reverse is likely to be true for corticosterone, which is thought to peak just before the onset of migratory flight (Piersma et al. 2000, Landys-Cianelli et al. 2002). High quality sites should be more likely to fully prepare a bird to migrate than low quality sites, and this difference should be larger for species exhibiting a migrate-then-molt strategy (most Semipalmated Sandpipers) because we would be more likely to capture a bird just prior to migration. We used linear densities of shorebirds at each site to examine whether shorebird behavior correlated with physiology, because density is a parameter often used to assess site quality from an observational perspective. We predicted that densities should be high where site quality is high, and this should correlate positively with

triglyceride and corticosterone levels (i.e., high densities = high levels of triglyceride and corticosterone). We also hypothesized that this correlation would be more significant for birds employing a molt-then-migrate strategy (most Dunlin) because site quality is likely to matter more to individuals spending longer periods of time at a given site. Lastly, we investigated whether patterns in site quality as assessed by physiological metrics are consistent across years; this has implications for long-term monitoring of sites using physiology as a tool.

4.3. Methods

4.3.1. Study area and field sites

We collected data from mid-July until early September at five (2005) or six (2006) field sites across the northern coast of Alaska (Fig. 4.2): Kasegaluk (70.301°N, 161.888°W; operated 2006 only), Peard Bay (70.812°N, 158.323°W), Point Barrow (71.290°N, 156.788°W), Colville (70.473°N, 150.564°W), Sagavanirktok (70.291°N, 148.202°W in 2005; moved to 70.246°N, 147.832°W in 2006), and Okpilak (70.080°N, 144.011°W). The Sagavanirktok site was decommissioned early (20 August) in 2006 due to bear activity. The field site locations were selected opportunistically based on (1) the presence of either a large lagoon system (Kasegaluk, Peard Bay, Point Barrow) or a large river delta (Colville, Sagavanirktok, Okpilak), both of which support large numbers of staging shorebirds, (2) the potential for logistical support from other project collaborators for

conducting work at the site, and (3) the ability to access the sites with fixed-wing aircraft or boats for deployment of personnel and equipment. Details on field season duration and camp activities are presented in Taylor et al. (2010).

Shorebird staging habitat in the northern Alaska region is a complex mosaic of brackish water mudflats and marsh; low-lying saline tundra; mud and gravel shores of sloughs, river deltas, and lagoons; and gravel mainland and barrier island beaches within 100-1000 m of the coastline (Johnson and Herter 1989). Tidal influence in the absence of storms is <10 cm vertical fluctuation, but wind-driven tidal intrusion is common during the ice-free period (July-September), resulting in brackish habitats well above normal high tide lines (Connors et al. 1979). Day length (sunrise to sunset) ranges from 24 hours in mid July to 15.5 hours on 1 September. Semipalmated Sandpiper and Dunlin are two of the most common shorebird species breeding and staging in this area; Western Sandpipers are common only in the western half of the study region (Kasegaluk, Peard Bay, and Point Barrow sites; Johnson et al. 2007).

4.3.2. Field methods

4.3.2.1. Shorebird captures

We captured postbreeding shorebirds at our field sites from mid-July to early September in each year of the study using mist nets and walk-in traps placed in areas where birds were actively foraging during daylight hours. Trapping was conducted opportunistically throughout the field season, but was restricted to suitable weather days

with light or no rain and wind conditions that enabled us to access sites where birds were foraging. Individuals were measured, weighed, banded, and blood-sampled within 45 minutes of capture and released back to the wild. We determined age by plumage characteristics (Prater et al. 1977), and scored molt by percent replacement of body feathers in five different regions (head, neck, back, breast, abdomen) according to this scale: 0 = no new feathers, 1 = <25% new feathers, 2 = approximately 50% new feathers, 3 = >50% but <75% new feathers, and 4 = >75% new feathers (Ginn and Melville 1983). We collected blood (approximately 300 μL) via brachial venipuncture, stored these samples on ice in the field, and centrifuged them within four hours of collection at 5000 rpm for 5 minutes with a portable centrifuge. The plasma was separated and either stored at -20°C immediately or frozen and transported in liquid nitrogen cryoshippers for up to a month, then stored at -20°C until assayed. We used samples where blood-sampling commenced after three minutes post-capture for triglyceride assay only, because standard corticosterone sampling protocols use a three-minute post-capture threshold for assessment of baseline corticosterone (reviewed in Romero and Reed [2004]). All capture and handling protocols were approved by the Institutional Animal Care and Use Committee at the University of Alaska Fairbanks (protocol # 04-31).

4.3.2.2. Shorebird surveys

At each field site, we established nine 1-km length transects within a 10-km diameter study area to assess postbreeding shorebird densities through time. Transects were not randomly placed, but rather were located where birds were observed foraging

when the field camp was established. Transects remained in the same locations throughout all years of the study. A single observer on foot surveyed all transects at a given site once every three days throughout each field season (24 July - 30 August 2005, 15 July - 4 September 2006). During each survey, we recorded all shorebirds observed within 200 m on either side of each transect.

4.3.3. Plasma assays

4.3.3.1. Triglyceride

We assayed plasma samples for triglyceride and free glycerol levels after both the 2005 and 2006 field seasons using sequential endpoint assay (Trinder reagents A and B, Sigma-Aldrich Canada, Oakville, Ontario) using 5 μL of plasma with 240 and 60 μL, respectively, of reagents A and B for free and total glycerol. We took readings for each metabolite with a microplate spectrophotometer at 540 nm after 10 min of incubation at 37°C following the addition of each reagent. Plasma triglyceride concentrations (in mmol/L) were calculated by subtracting free glycerol (reagent A) from total glycerol (reagent B). We ran assays in 400-μL flat-bottom 96-well microplates (NUNC, Denmark). Each plate was run with a standard curve based on a serial dilution of 2.54 mmol glycerol (Sigma-Aldrich). In 2005, intra-assay coefficients of variation (CVs) were 12.27% and 8.67% for free and total glycerol, respectively; in 2006 intra-assay CVs were 3.87% and 4.77%. We used a 19-day-old hen plasma pool to calculate the inter-assay CV in 2005, whereas in 2006 we calculated the inter-assay CV using a plasma pool

from the Sigma-Aldrich glycerol standard. Inter-assay CVs across years were 13.03% and 10.98% for free and total glycerol, respectively (n=16).

4.3.3.2. Corticosterone

Blood samples were not collected quickly enough to assess baseline corticosterone levels in 2005. In 2006, we assayed blood samples for baseline corticosterone levels using radioimmunoassay (RIA, Wingfield et al. 1992), which involves 1) the extraction of plasma steroids with dichloromethane and 2) competitive binding between corticosterone in the sample and radioactively-labeled synthetic corticosterone. Specifically, we pipetted 20 µl of each plasma sample into glass centrifuge tubes, to which we added 180 µl distilled water and a small amount of radioactively labeled steroid (2000 cpm). This mixture was allowed to calibrate overnight at 4°C. We extracted the steroid fraction of each sample with distilled dichloromethane, dried it under nitrogen gas, and resuspended it in 550 µl phosphate-buffered saline solution with 0.1% gelatin. We then assayed duplicate samples of 200 µl by RIA. We created a standard curve using synthetic, non-radioactive corticosterone (ranging from 7.8-2000 pg/ml) and used this to assess the amount of natural corticosterone in each plasma sample. The percentage recovery of steroid by extraction was estimated by measuring total cpm in 100 µl of the remaining steroid + buffer mixture. We then adjusted the amount of unknown (natural) corticosterone in each plasma sample by the percentage recovery for that sample. Average recoveries for Semipalmated Sandpiper, Western Sandpiper, and Dunlin were 91.85 ± 4.58%, 91.01 ±

3.97%, and 89.30 ± 2.81%, respectively; intra-assay CVs for these same species were 2.96%, 1.78%, and 9.60%. We used a standard of 1.0 ng corticosterone to calculate the inter-assay CV, which was 6.89% across all assays (n=5).

4.3.4. Data analysis

We first used ANOVA to examine variation in molt intensity and date of capture by species. We averaged molt scores for each individual across five body regions (head, neck, back, breast, abdomen) to arrive at a single molt intensity score, which was an integer value calculated from a set of ordinal values. These molt intensity scores were then used to examine the hypothesis that our three study species were undergoing the level of active molt we expected based on their published life history information. We also examined correlations between molt intensity and date of capture to determine how the relative level of molt for each species changed through time.

We next used a set of *a priori* linear models for each species to examine whether and how triglyceride and corticosterone levels varied by site, year, and date of capture. We analyzed species separately due to the inherent expectation that absolute values for triglyceride and/or corticosterone levels may not be directly comparable across species (Cockrem 2004). We did not analyze free glycerol levels because these have been found to be less informative than triglyceride levels for assessing site-specific differences in refueling rates in previous studies of migratory shorebirds (Guglielmo et al. 2002, Acevedo Seaman et al. 2006). We did not control for sex in our analyses because

previous studies have found no influence of sex on triglyceride or corticosterone levels in shorebirds during autumn migration (Guglielmo et al. 2002, O'Reilly and Wingfield 2003, Acevedo Seaman et al. 2006). Captured individuals differed widely in structural body size, and within a species, larger shorebirds are known to have higher basal triglyceride levels (Williams et al. 1999). Therefore, we used tarsus length as a covariate in all body mass analyses; i.e., we analyzed size-corrected body mass (Acevedo Seaman et al. 2006). In all candidate models for triglyceride, we additionally controlled for the effect of bleed time (time between capture and blood sampling for a given individual) because this variable affects triglyceride levels in migrating shorebirds (Acevedo Seaman et al. 2006, Williams et al. 2007). We did not control for bleed time in corticosterone analysis because we limited our analysis to those samples collected within three minutes of capture. Shapiro-Wilk tests revealed non-normality in the distributions of the response variables (W[triglyceride]=0.8705, W[baseline corticosterone]=0.8622, both $p<0.001$) thus we used log(metric)+1 to normalize these variables for all subsequent analyses. We used Akaike's Information Criterion corrected for small sample sizes (AIC_c) to select among competing models for the one that most realistically described relationships between the independent variables and physiological responses (Burnham and Anderson 2002). If the AIC_c-based model selection process identified more than one model as having substantial support given the data, we dealt with model selection uncertainty by averaging across all models within 10% of the Akaike weight of the top model. We examined the weight of evidence (using summed Akaike weights and estimated

regression coefficients for the site, capture date, and the site by year interaction parameters) for our *a priori* hypotheses for site-specific differences in physiologic metrics, trends in physiology through time, and whether differences in physiologic metrics were consistent through years, respectively. We used regression coefficients and 95% confidence intervals (model-averaged if applicable) to examine effect sizes for specific parameters. To investigate the singular effect of molt intensity on physiological metrics, we added the molt intensity variable to the best model and determined the direction and magnitude of change in AIC_c. Comparing the AIC_c values for the best model and the best model + molt intensity should provide an asymptotically unbiased estimate of the difference in Kulback-Liebler information provided by each model; a model with a lower AIC_c would then be closer to the unknown "true" model giving rise to the data (Burnham and Anderson 2002) .

To compare the relative density of postbreeding shorebirds among field sites, we first calculated a linear density for each species and site during each three-day survey period by dividing the number of individuals of each species observed by the total number of transects surveyed. Next we calculated the mean linear density of each species at each site over all the survey periods. Because the linear density data were derived from counts of individuals and tended to be overdispersed (variance > mean), we used quasi-Poisson regression (O'Hara and Kotze 2010) to compare mean densities across sites in each year for each species. We did not attempt to correct the raw survey data for detectability because it was easy to observe shorebirds in the vegetation-free

littoral areas of our study area, thus we believe detectability as a function of distance from the observer was relatively constant (although potentially biased low). This does not present a problem because all sites had similar habitat conditions and were surveyed using the same methodology, making comparisons across sites possible. However, our emphasis for this research is on comparative bird use, not absolute abundances.

Lastly, we examined the strength and direction of relationships between site-specific triglyceride, corticosterone, and linear density for each species and year combination by performing a Spearman's rank correlation analysis between paired site means for two variables at a time.

All analyses were conducted in RExcel (Baier and Neuwirth 2007) running R version 2.11.1 (R Foundation for Statistical Computing 2010).

4.4. Results

We captured a total of 629 shorebirds of all three species throughout the study; sample sizes of each species at each site and in each year varied widely (Table 4.1). For each species, we describe levels of molt intensity and date of capture, patterns in physiological metrics across sites, site-specific shorebird densities, and relationships between these variables.

4.4.1. Variation in molt intensity and date of capture

Molt intensity scores were highly variable across species (Fig. 4.3), but on average molt intensity scores for Dunlin were 1.02 units (95% C.I. = 0.66, 1.39) higher than Western Sandpipers and 1.97 units (95% C.I. = 1.63, 2.30) higher than Semipalmated Sandpipers. There was also a significant year effect ($F_{1,600} = 108.52, p < 0.001$): molt intensity scores for all species combined were lower in 2006 than in 2005 by 1.47 units (95% C.I. = 1.11, 1.83) but there was no species by year interaction. We found a small but significant negative correlation with capture date for Dunlin (Spearman $\rho = -0.31, p = 0.008$), indicating a decline in molt intensity through time as we predicted if individuals were completing prebasic molt throughout the postbreeding season. There was a marginally significant negative correlation for Western Sandpipers ($\rho = -0.15, p = 0.064$), and no significant correlation for Semipalmated Sandpipers ($\rho = -0.06, p = 0.215$)(Fig. 4.3).

Capture dates varied by species ($F_{2,623} = 20.83, p < 0.001$) and year ($F_{1,623} = 39.80, p < 0.001$). In 2005, Semipalmated Sandpipers were captured on average 6.2 days (95% C.I. = 2.4, 10.1) earlier than Dunlin and 8.0 days (95% C.I. = 5.1, 10.9) earlier than Western Sandpipers. There was no significant difference between capture dates of Western Sandpipers and Dunlin. In 2006, Semipalmated Sandpipers were captured 20.2 days (95% C.I. = 17.6, 22.8) earlier than Dunlin and 10.5 days (95% C.I. = 8.6, 12.4) earlier than Western Sandpipers. Western Sandpipers were captured 9.7 days (95% C.I. = 6.8, 12.7) earlier than Dunlin.

We also examined whether date of capture varied by site within each species (Fig. 4.4). Capture dates for Dunlin increased by 11.6 days (95% C.I. = 3.4, 19.9) from west to east in 2006 (excluding Sagavanirktok where data collection ended early) when this species was captured at most sites. Semipalmated Sandpipers were captured in both years of the study at all sites except Kasegaluk (which was not active in 2005); capture dates increased from west to east by 13.2 days in 2005 (95% C.I. = 6.4, 20.0) and by 3.1 days (95% C.I. = 0.1, 6.2) in 2006. Capture dates for Western Sandpipers increased 13.7 days (95% C.I. = 5.8, 21.5) from west to east in 2006 (excluding Sagavanirktok), when this species was captured at all sites.

4.4.2. Triglyceride levels

4.4.2.1. Dunlin

There was a high degree of uncertainty in modeling triglyceride levels in Dunlin, with nine models falling within 10% of the Akaike weight of the top-ranked model (Table 4.2). Site was included in six of the nine top models (but not the top model); together these models carried 62% of the Akaike weight for the model set. Date of capture was included in the top model plus four others, which in total carried 52% of the Akaike weight. The site by year interaction effect was only included in one model in the set, which carried only 5% of the Akaike weight. Most 95% confidence intervals for model-averaged coefficients overlapped 0, but triglyceride levels were substantially lower at Peard Bay (θ_{Peard} = -0.310, 95% C.I. = -0.572, -0.049)(Fig. 4.5) compared to all

other sites. Triglyceride levels increased with date of capture in 2006 but not in 2005 ($\theta_{2006*Date}$ = 0.024, 95% C.I. = 0.005, 0.044). The model-averaged regression coefficient for the site by year parameter overlapped 0.

4.4.2.2. Semipalmated Sandpiper

There was less uncertainty in the model selection process for triglyceride levels in Semipalmated Sandpipers: only four models fell within 10% of the Akaike weight of the top model (Table 4.2). Site was included in all of the top models. Capture date was included in two of the four, which in total carried 66% of the model weight. The site by year interaction effect was not included in any of the top models for triglyceride levels. All 95% confidence intervals for model-averaged coefficients of site parameters overlapped 0, although triglyceride levels appeared to be marginally higher at Point Barrow (θ_{Barrow} = 0.110, 95% C.I. = -0.001, 0.221), particularly in 2005, than at other sites (Fig. 4.5). Triglyceride levels increased slightly with capture date (θ_{Date} = 0.004, 95% C.I. = 0, 0.008).

4.4.2.3. Western Sandpiper

Three models for triglyceride levels in Western Sandpipers fell within 10% of the Akaike weight of the top model (Table 4.2); site was included in all of the top models. Capture date was included in only the second model, which accounted for 24% of the Akaike weight. The site by year interaction effect was included in the third best model, and carried 18% of the Akaike weight. Despite site being included in all of the top models, 95% confidence intervals for all model-averaged coefficients of site parameters

overlapped 0. Capture date had a negligible effect on triglyceride levels. Although the site by year interaction was not significant, triglyceride levels were substantially higher across all sites higher in 2006 than in 2005 (θ_{2006} = 0.222, 95% C.I. = 0.115, 0.330) (Fig. 4.5).

4.4.2.4. Effect of molt intensity

Adding the molt intensity variable improved the fit of the best model for Dunlin and Western Sandpipers by 3.03 and 1.58 AIC_c units, respectively, but did not improve the fit of the best model for Semipalmated Sandpipers (Table 4.2). Triglyceride levels decreased with increasing molt intensity for Dunlin ($\beta_{Moltscore}$ = -0.067, 95% C.I. = -0.126, -0.009) but the confidence interval for the coefficient overlapped 0 for Western Sandpiper.

4.4.3. Corticosterone levels

The candidate set of linear models was reduced from twelve to five for baseline corticosterone analysis, and we could not test for a site by year interaction effect because we had data from a single year (2006) instead of two.

4.4.3.1. Dunlin

Models for corticosterone levels in Dunlin performed poorly overall ($R^2 < 0.1$), likely due to small sample sizes. There was a high degree of model uncertainty: four of the five models were within 10% of the Akaike weight of the top model (Table 4.3). Site was included in two of the four top models, which accounted for 54% of the Akaike

weight of the model set. Capture date was included in the third and fourth best models, which accounted for 22% of the Akaike weight. However, all model-averaged regression coefficients for site and capture date parameters overlapped 0.

4.4.3.2. Semipalmated Sandpiper

Two models for corticosterone levels in Semipalmated Sandpipers were within 10% of the Akaike weight of the top model (Table 4.3). Site was included in both top models. Capture date was included in the top model, which accounted for 59% of the Akaike weight of the model set. Corticosterone levels were substantially lower at Peard Bay (θ_{Peard} = -0.354, 95% C.I. = -0.570, -0.139) and higher at Colville ($\theta_{Colville}$ = 0.480, 95% C.I. = 0.287, 0.673) than at other sites (Fig. 4.5). Corticosterone levels increased marginally with date of capture (θ_{Date} = 0.005, 95% C.I. = -0.001, 0.012).

4.4.3.3. Western Sandpiper

Models examining corticosterone levels in Western Sandpipers performed poorly ($R^2 < 0.1$), and there was a high degree of model selection uncertainty (Table 4.3). Site was included in the third and fourth best models, which accounted for 16.8% of the Akaike weight of the model set. Capture date was included in the second and third best models, which accounted for 52 % of the Akaike weight. However, all model-averaged regression coefficients for site and capture date parameters overlapped 0.

4.4.3.4. Effect of molt intensity

Adding the molt intensity parameter to the best model for any species did not improve the fit (Table 4.3).

4.4.4. Shorebird densities

Linear densities for Dunlin varied by site ($F_{5,115} = 23.93, p < 0.001$), and there was a significant site by year interaction ($F_{4,110} = 4.73, p = 0.001$), although Colville showed the highest densities of Dunlin in both years (Fig. 4.5). Linear densities for Semipalmated Sandpipers also varied by site ($F_{5,115} = 5.97, p < 0.001$) with a significant site by year interaction ($F_{4,110} = 2.92, p = 0.025$). Semipalmated Sandpiper density was high at the Colville site in 2005 and at the Colville and Sagavanirktok sites in 2006 (Fig. 4.5). Western Sandpiper linear densities varied both by site ($F_{2,58} = 15.63, p < 0.001$) and year ($F_{1,57} = 7.16, p = 0.010$) but there was no evidence of a site by year interaction. Western Sandpiper densities at the Kasegaluk site in 2006 were higher than the Peard Bay or Point Barrow sites, which had similar densities in both 2005 and 2006 (Fig. 4.5).

4.4.5. Relationship between physiological metrics and density

Correlations between site-specific mean triglyceride levels and linear densities were negative but non-significant for all species in both years (Fig. 4.6). Semipalmated Sandpipers showed a positive relationship between mean site-specific corticosterone levels and linear density in 2006 (Spearman $\rho = 0.94, p = 0.017$), but this relationship was not observed for other species (Fig. 4.6).

4.5. Discussion

4.5.1. Effect of molt strategy on physiology

We hypothesized that the three species we studied would show differences in mean molt intensity and capture dates as a result of known species-specific differences in molt strategy (when prebasic molt occurs in relation to fall migration). In accordance with this hypothesis, average molt intensity was higher in Dunlin than in Western Sandpipers, which were in turn higher than Semipalmated Sandpipers. Molt intensity also showed a significant decline throughout the postbreeding period for Dunlin only. On average, Semipalmated Sandpipers were captured earlier than either of the other two species in both years. Dunlin and Western Sandpipers had similar mean capture dates in 2005, but Dunlin were captured approximately ten days later than Western Sandpipers in 2006. This matches previously reported patterns of residence time by radio-equipped birds at postbreeding sites (Chapter 3). These species-specific patterns of molt intensity and capture dates confirm that the sample of birds for which we tested physiological parameters conform to expected differences in molt strategy; namely, that Dunlin exhibited a molt-then-migrate strategy whereas Semipalmated Sandpipers exhibited a migrate-then-molt strategy. Western Sandpipers appeared to be intermediate in strategy, although the source of the variation (i.e., from individual variation in molt timing or an intermediate strategy across the population) is not clear.

Previous studies indicated that molt intensity had a negative influence on triglyceride levels in both passerines and shorebirds (Totzke and Bairlein 1998, Jenni-Eiermann et al. 2002). To date, no studies have tested the influence of molt on corticosterone levels in shorebirds, although baseline corticosterone levels appear to be downregulated in molting passerines (Romero 2002). We expected that molt intensity would show a negative relationship with both triglyceride and corticosterone levels in all species, and that the size of this effect would be greater for Dunlin than for Western or Semipalmated Sandpipers. We found little evidence that molt intensity was negatively related to corticosterone levels: adding the molt intensity variable to the best linear model for corticosterone did not improve the fit for any species. We suggest that unlike most granivorous passerines, shorebirds feeding on invertebrate prey may not be protein limited during prebasic molt. Thus for shorebird species, selection may be limited to downregulate cortiscosterone at the expense of using this hormone to facilitate pre-migratory fattening or the transition from postbreeding to migratory condition for shorebird species.

However, molt intensity did improve the fit of the best model for triglyceride for both Dunlin and Western Sandpipers (but not Semipalmated Sandpipers), and triglyceride levels decreased with increasing molt intensity. These effects were greater for Dunlin than for Western Sandpipers. Refueling rates are likely to be depressed in birds undergoing active body molt, because molt and pre-migratory fueling are both energetically demanding processes. Lipids may have been used to fuel feather

production during molt and were therefore less available for storage as fuel reserves in captive Red Knots (Jenni-Eiermann et al. 2002). In contrast, although they did not measure triglyceride levels specifically, Holmgren et al. (1993a) reported no effect of wing molt on the rate of body mass change in adult Dunlin. This may have been because molt intensity in the birds they captured was less than would be typical for stationary Dunlin at actual molting sites (Holmgren et al. 1993b) and was not a major source of energetic competition with refueling activity. Alternatively, the effects of body feather vs. wing molt on lipid availability or body mass change may not be the same. We were not able to test whether there was an increase in triglyceride levels for either Dunlin or Western Sandpipers toward the end of the postbreeding period, when most birds should have completed molt and potentially switched to pre-migratory fuel deposition. Adult pre-migratory Catbirds (*Dumatella carolinensis*), a passerine species, exhibited slow rates of fuel deposition during prebasic molt, but became hyperphagic and deposited fuel reserves quickly just prior to migration, when molt was completed (Heise and Moore 2003). This pattern could be tested in the future in individual captive or recaptured free-living postbreeding shorebirds using triglycerides as an index of fuel deposition rate.

Finally, we also hypothesized that date of capture was likely to have a larger effect on physiological parameters for species with a molt-then-migrate strategy, which remain at postbreeding sites for longer prior to fall migration. Model-averaged regression coefficients upheld this expectation for triglyceride levels in Dunlin vs. Semipalmated Sandpipers: estimated effect size of the capture date parameter on

triglyceride levels was six times greater for Dunlin than for Semipalmated Sandpipers, indicating that triglyceride levels in Dunlin increased more through time than for Semipalmated Sandpipers. Assuming that triglyceride levels are indicative of fuel deposition rate (Williams et al. 1999), these results indicate that Dunlin increased their fueling rates more throughout the postbreeding period than other species, consistent with the previously published theory that Dunlin are using postbreeding sites in northern Alaska for staging (e.g., replenishing depleted fuel reserves after molt; Chapter 3).

4.5.2. Assessment of site quality via physiological metrics

We hypothesized that physiological metrics (triglyceride and corticosterone) would reflect variation in fueling rates and migratory readiness, and these relationships would depend on an individual's molt strategy. Taken at a population level, variation in physiological metrics should reflect site quality in the context of species-specific molt strategy. Our model selection analysis suggested some site-specific variation in both triglyceride and corticosterone levels for all species across both years of the study, as evidenced by site being included in the best model set for triglyceride levels in all species and for corticosterone levels in Dunlin and Semipalmated Sandpipers. Two specific patterns indicating site quality did emerge: (1) triglyceride levels were low for Dunlin at Peard Bay and marginally high for Semipalmated Sandpipers at Point Barrow; and (2) corticosterone levels were low at Peard Bay and high at Colville for Semipalmated Sandpipers.

We hypothesized that we would see a larger effect of site on triglyceride levels in species with a molt-then-migrate strategy (most Dunlin) because site quality should be more important to species that spend a longer period of time at postbreeding sites. We actually observed the smallest effect of site on triglyceride levels for Dunlin (the site parameter occurred in models containing 62% of the Akaike weight of the model set, in contrast to 100% for Semipalmated and Western Sandpipers), contrary to our expectation. However, the magnitude of the differences between sites was consistent with our hypothesis of a larger effect of site on triglyceride levels in molt-then-migrate species. For Dunlin, log-transformed triglyceride levels at Peard Bay were 0.310 mmol/L lower than other sites, whereas triglyceride levels for Semipalmated Sandpipers at Point Barrow were only 0.110 mmol/L higher than at other sites.

In accordance with our hypothesis that we would observe a larger effect of site in species that exhibit a migrate-then-molt strategy, site had the largest influence on corticosterone levels in Semipalmated Sandpipers (site parameter appeared in all models for Semipalmated Sandpipers, in models containing 54% of the Akaike weight for Dunlin, and in models containing 17% of the Akaike weight for Western Sandpipers). Additionally, the magnitude of the differences between sites was congruent with our expectation: log-transformed triglyceride levels at Peard Bay were substantially lower (by 0.354 mmol/L) than at other sites, and levels at Colville were substantially higher (by 0.480 mmol/L).

The utility of using triglyceride levels to assess site quality at Arctic postbreeding areas has not been examined previously, and we know of no other study that has used corticosterone to assess site quality for any system. An advantage we had in this study was the ability to use linear density as an independent measure of site quality in the absence of detailed data on food availability or fueling rates (mass gain through time) across our sites. We assumed that high densities equated to high quality foraging sites, because postbreeding shorebirds should be under selection to either acquire fuel for migration or for regrowing feathers. For all species, we hypothesized that triglyceride levels should be higher at sites where linear densities were higher, although the strength of this relationship should vary by molt strategy because site quality is likely to be more important to birds that will remain at a given site during molting and pre-migratory fattening. Our results showed no species-specific differences in the strength of the relationship, although for all species, triglyceride levels did show a non-significant decrease with increasing density. Given that we observed evidence of differences in molt strategy across species and that these differences are likely to mediate behavior (indicated by density) through physiology, this finding may indicate either (a) large variation in site-specific triglyceride levels and/or densities such that correlations on a species level are not observed, or (b) that linear density is not a good predictor of site quality. One possible explanation for (a) could be that shorebirds are capable of depleting food resources at some foraging sites where densities are high (e.g., Schneider and Harrington 1981), and thus triglyceride levels could actually be lower if resource depletion occurs

during the postbreeding period. A scenario of early resource depletion may be plausible in a late-summer Arctic environment where predation pressure from shorebirds is combined with deteriorating weather conditions. If resource depletion were occurring, mean triglyceride levels would be intermediate where densities were high. This may have been the case at the Colville site: densities at this site were highest in both years of the study for Dunlin and Semipalmated Sandpipers, yet Colville had intermediate triglyceride levels for both species in both years. Alternatively, the latter explanation (b) may certainly bear weight: density may not be an appropriate variable for assessing habitat quality particularly for patchy, seasonal habitat or generalist species, although it may be a good indicator if surveys can be stratified accordingly (Van Horne 1983).

We also hypothesized that corticosterone levels should be higher at sites where densities were higher, and that again, this relationship should be stronger for species that were molting and thus remained at postbreeding sites for longer. In contrast to our expectation, we found no relationship between corticosterone and linear density for Dunlin or Western Sandpipers, but in Semipalmated Sandpipers corticosterone did increase with increasing linear density. This may make sense given our results from evaluating the function of postbreeding sites for each of our study species. Semipalmated Sandpipers are likely to be just stopping over at postbreeding sites on the coast of northern Alaska, briefly resting between flights rather than staging while completing molt and acquiring fuel for migration (like Dunlin; Chapter 3). Under this scenario, high quality sites may be those where food resources are adequate to allow an individual to

rest and briefly refuel in order to continue its migration, thus Semipalmated Sandpipers captured at these sites should have high mean corticosterone levels characteristic of birds about to depart for migratory flights (Landys-Cianelli et al. 2002, O'Reilly and Wingfield 2003). In contrast, lower quality sites might be those at which individuals need to stop for longer to acquire the needed fuel resources, thus mean corticosterone levels should be lower if an average bird captured at these sites is less likely to be about to commence migratory flight.

Lastly, we did an exploratory analysis of whether site-specific differences in triglyceride levels were consistent across years, which would be a useful characteristic if a physiological metric could be used as a monitoring tool for site or habitat quality through time. Based on the importance of the site by year interaction parameter in the *a priori* model sets (site by year parameter appeared in no models for Semipalmated Sandpipers, in models containing only 5% of the Akaike weight for Dunlin, and in models containing 17% of the Akaike weight for Western Sandpipers), we found little evidence that the relationship between the sites with respect to triglyceride levels varied between years, although triglyceride levels in Western Sandpipers were overall higher in 2006 than in 2005. One possible reason for the larger effect of year and the site by year interaction for Western Sandpipers might be that the proportion of individuals within the population that employed the migrate-then-molt vs. molt-then-migrate strategies may have changed between the two years, thus overall population use of postbreeding sites varied in a way that we were not able to predict and test.

4.5.3. Effects of migratory stage, time of year, and age: implications for interpretation of physiology

As demonstrated in this study, physiological metrics may vary temporally depending on the timing of sampling relative to the timing of life history events. We conducted our research during the postbreeding period because this stage in the life cycle of Arctic breeding shorebirds in North America has not been well studied. However, this posed some issues for hypothesizing possible relationships between site quality and physiology. Most studies using plasma metabolites like triglyceride to assess refueling rates and site quality were conducted at stopover sites along the migration route (e.g., Guglielmo et al. 2005, Acevedo Seaman et al. 2006, Williams et al. 2007), when it was known that all individuals sampled had flown some distance to get to a particular site. In our study system, the postbreeding period represented shorebirds in transition from the breeding to migratory life history stage. Sampled individuals may have already begun migration, been about to migrate, or were staging depending on the species and individual; these discrepancies in migratory stage almost certainly affected each individual's physiology and introduced variability into our data. A number of studies have reported that corticosterone levels were negatively related to body condition of birds (e.g., Schwabl et al. 1991, Holberton et al. 1999, Kitaysky et al. 1999). Many studies reporting a negative relationship between corticosterone and body condition were done on birds at breeding or wintering sites rather than during migration. We argue that for migratory or pre-migratory birds, corticosterone is likely to be more closely tied to migratory state and

how close an individual is to departing on true migration (Landys-Cianelli et al. 2002, O'Reilly and Wingfield 2003). A secondary link to body condition within a given migratory state may exist, although we did not examine this in our study. A controlled experiment using birds of different migratory states whose body condition could be manipulated through diet would be useful to examine how covariation in these parameters affects corticosterone levels. Lastly, Lindstrom et al. (2002) found evidence to support that juvenile shorebirds in the high Arctic depart breeding areas with low fuel stores, consistent with a time-minimizing strategy and the expectation that fueling rates will increase away from the breeding grounds. This finding has implications for the function of postbreeding sites for the juvenile shorebirds we studied: even those that are may be considered to be staging in northern Alaska may be doing so without adhering to the recognized definition of the term (storing fat mass in excess of 40% of lean body mass; Warnock 2010). If postbreeding shorebirds are not acquiring large fuel stores prior to migration, there may not be much selective pressure to choose foraging sites based on maximum fueling rates. These documented differences in behavior and selective forces across migratory stage, time of year, and even age groups highlight that comparisons of physiology across individuals, sites, or time periods are relatively meaningless without an understanding of the various life history strategies being represented.

4.5.4. Conclusions: utility of using physiology to examine site function and quality

We were able to show that physiological metrics do vary predictably between species that exhibit different life history (molt) strategies and thus use the same habitats for different purposes and lengths of time. Our results also showed there were consistent differences in physiologic metrics between sites across years, and these differences were correlated with an independent measure of site quality (linear density) for at least one metric in one species.

If physiological metrics provide an index of site quality that reflects true differences in performance of birds at a site, and that index can be obtained by capturing individual birds a single time, this technique could provide a relatively low-cost and efficient means of assessing landscape-scale variation in habitat use, and enable large-scale comparisons of sites or habitats for management or conservation purposes. Acevedo Seaman et al. (2006) found a positive relationship between triglyceride levels and total macrofaunal prey abundance during northbound migration, indicating that birds captured at sites with higher food availability tended to have higher fuel deposition rates. In both their study and in ours, the study sites were sampled to some degree serially, for logistic reasons as well as the temporal nature of shorebird migration across large areas. Thus both triglyceride levels and measures of site quality (e.g., macrofaunal prey abundance or density) may have covaried with date. However, the spatial pattern of site differences in triglyceride levels in Acevedo Seaman et al.'s study did not match site-

specific differences in mean dates of capture. In our study, triglyceride levels did not appear to increase (within each species) going from west to east across the study area (see Fig. 4.5) although capture dates did. Both studies therefore provide evidence that site-specific triglyceride levels are to some degree reflective of true site differences in fuel deposition rates, rather than an artifact of temporal trends in fattening that are expected prior to fall migration.

For physiological assessment techniques to be effective, researchers must match sampling efforts with the time scale over which migratory birds change life history states or make decisions about staying at or leaving a given site. Whether birds have just arrived or are preparing to depart may affect their physiological state (e.g., refueling vs. leveling off mass gain in preparation for flight, corticosterone stimulating hyperphagia or migratory preparedness) as much or more than site quality. Williams et al. (2007) found that in Western Sandpipers on northbound migration, triglyceride levels were not related to prey availability (invertebrate densities) and thus showed evidence of birds increasing fueling rates for reasons other than better habitat quality as they migrated north. Additionally, birds must remain at a given site for long enough that a bird sampled for its physiological profile at that site will not have just arrived from another site, such that its profile level reflects site quality elsewhere. Post-capture residence time estimates for postbreeding shorebirds on the coast of northern Alaska were 4.5 to 13.9 days on average, depending on species (Chapter 3). Therefore it is likely that the majority of

birds we sampled for physiological metrics had been at the location where we sampled them for long enough that their profiles reflected site-specific quality.

The ease with which physiologic metrics may be used to assess habitat quality is appealing: if a rapid assessment of comparative site function or quality is needed, it may be simpler to capture staging shorebirds for blood sampling and conduct the subsequent laboratory assays than to attempt a field-based assessment of food availability or a series of broad-based surveys for comparative shorebird abundance. The former requires knowledge of invertebrate taxonomy, distribution, and diversity in order to design an appropriately scaled study, and the necessary data is time-consuming to collect and analyze. Aerial or ground surveys across a large area can be costly, weather-dependent, and subject to bias from a mismatch between temporal spacing of the surveys and the length of time over which birds use or move across a landscape (e.g., Taylor et al. 2010). However, despite the temptation to use plasma metabolites or hormone levels to explore differences between sites in terms of function or quality, we suggest that physiologic metrics might be better used as a confirmatory analysis for predicted site quality differences or for use as a monitoring method for long-term changes in habitat quality that are suggested by other research. Initial (exploratory) assessments of site quality via physiology might be well-served by using multiple species and multiple physiologic metrics to examine commonalities in patterns of site-specific differences. Placing physiologic metrics into the context of variable life history strategies, behavior, migratory stage or age differences, and species-specific ecology is necessary to make a causal link

between distribution and physiology. Individual-based predictive modeling of site quality based on vital rates (e.g. Stillman et al. 2005) coupled with confirmatory physiologic assessments and monitoring of plasma metabolites or hormone levels could provide a long-term method for evaluating changes in site function and quality.

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4.7. Literature cited

Acevedo Seaman, D.A., C.G. Guglielmo, R.W. Elner, and T.D. Williams. 2006. Landscape-scale physiology: site differences in refueling rates indicated by plasma metabolite analysis in free-living migratory sandpipers. Auk 123:563-574.

Alerstam, T., and A. Lindstrom. 1990. Optimal bird migration: the relative importance of time, energy, and safety. In: E. Gwinner, Ed. Bird Migration: Physiology and Ecophysiology. Berlin: Springer-Verlag.

Andres, B.A. 1994. Coastal zone use by postbreeding shorebirds in northern Alaska. Journal of Wildlife Management 558:206-213.

Baier, T., and E. Neuwirth. 2007. Excel :: COM :: R. Computational Statistics 22:91-108.

Berthold, P. 1975. Migration: control and metabolic physiology. In: D.S. Farner, J.R. King, and K.C. Parkes, eds. Avian Biology V. New York: Academic Press.

Burnham, K.P., and Anderson, D.R. 2002. Model selection and inference: a practical information-theoretic approach, second edition. New York: Springer-Verlag.

Cherel, Y., J. Leloup, and Y. Le Maho. 1988. Fasting in King Penguin II: hormonal and metabolic changes during molt. American Journal of Physiology 254:R178-R184.

Chown, S.L., K.J. Gaston, and D. Robinson. 2004. Macrophysiology: large-scale patterns in physiological traits and their ecological implications. Functional Ecology 18:159-167.

Cockrem, J.F. 2004. Conservation and behavioral neuroendocrinology. Hormones and Behavior 48: 492–501.

Connors, P.G. 1984. Ecology of shorebirds in the Alaskan Beaufort littoral zone. In: R. Barnes, D.M. Shell, and E. Ramirez, E., eds. The Alaskan Beaufort Sea: Ecosystems and environments. New York: Academic Press.

Connors, P.G., J.P. Myers, and F.A. Pitelka 1979. Seasonal habitat use by Arctic Alaskan shorebirds. Studies in Avian Biology 2:101–111.

Cramp, S. and K. E. L. Simmons. 1983. The birds of the Western Palearctic, Volume 3. Oxford: Oxford University Press.

Ginn, H. B., and D. S. Melville. 1983. Molt in birds. British Trust for Ornithology Guide 19. Tring, England: Maud and Irvine Ltd.

Guglielmo, C.G., P.D. O'Hara, and T.D. Williams. 2002. Extrinsic and intrinsic sources of variation in plasma lipid metabolites of free-living western sandpipers (*Calidris mauri*). Auk 119:437-445.

Guglielmo, C.G., D.J. Cerasale, and C. Eldermire. 2005. A field validation of plasma metabolite profiling to assess refueling performance of migratory birds. Physiological and Biochemical Zoology 78:116-125.

Heise, C.D., and F.R. Moore. 2003. Age-related differences in foraging efficiency, molt, and fat deposition of gray catbirds prior to autumn migration. Condor 105:496-504.

Hicklin, Peter and Cheri L. Gratto-Trevor. 2010. Semipalmated Sandpiper (*Calidris pusilla*). In: A. Poole, eds. The Birds of North America Online. Ithaca: Cornell Lab of Ornithology; retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/006doi:10.2173/bna.6

Holberton, R.L., P.P. Marra, and F.R. Moore. 1999. Endocrine aspects of physiological condition, weatherm, and habitat quality in landvbird migrants during the non-breeding period. In: N.J. Adams and R.H. Slotow, eds. Proceedings of the 22nd International Ornithological Congress:847-866. Johannesburg: BirdLife South Africa.

Holberton, R.L., J.D. Parrish, and J.C. Wingfield. 1996. Modulation of the adrenocortical stress response in neotropical migrants during autumn migration. Auk 113:558-564.

Holmes, R.T. 1966. Molt cycle of the Red-backed Sandpiper (*Caldris alpina*) in western North America. Auk 83:517-533.

Holmes, R.T. 1971. Latitudinal differences in the breeding and molt schedules of Alaskan Red-backed Sandpipers (*Calidris alpina*). Condor 73:93-99.

Holmes, R.T. 1972. Ecological factors influencing the breeding season schedule of Western Sandpipers (*Calidris mauri*) in subarctic Alaska. American Midland Naturalist 87:472-491.

Holmgren, N., H. Ellegren, and J. Pettersson. 1993a. Stopover length, body mass, and fuel deposition rate in autimn migrating adult Dunlins *Calidris alpina*: evaluating the effects of moulting status and age. Ardea 81:9-20.

Holmgren, N., H. Ellegren, and J. Pettersson. 1993b. The adaptation of moult pattern in migratory Dunlins *Calidris alpina*. Ornis Scandinavica 24:21-27.

Homyack, J.A. 2010. Evaluating habitat quality of vertebrates using conservation physiology tools. Wildlife Research 37:332-342.

Hutto, R. L. 1985. Seasonal changes in the habitat distribution of transient insectivorous birds in Southeastern Arizona: Competition mediated? Auk 102:120–132.

Jenni-Eiermann, S., and L Jenni. 1996. Metabolic differences between the postbreeding, moulting, and migratory periods in feeding and fasting passerine birds. Functional Ecology 10:62-72.

Jenni-Eiermann, S., L Jenni, and T Piersma. 2002. Plasma metabolites reflect seasonally changing metabolic processes in a long-distance migrant shorebird (*Calidris canutus*). Zoology 105:239-246.

Johnson, S.R., and D.R. Herter. 1989. The birds of the Beaufort Sea. Anchorage: BP Exploration (Alaska), Inc.

Johnson, J.A., R.B. Lanctot, B.A. Andres, J.R. Bart, S.C. Brown, S.J. Kendall, and D.C. Payer. 2007. Distribution of breeding shorebirds on the Arctic Coastal Plain of Alaska. Arctic 60:277-293.

Kitaysky, A.S., J.C. Wingfield, and J.F. Piatt. 1999. Dynamics of food availability, body condition, and physiological stress response in breeding Black-legged Kittiwakes. Functional Ecology 13:577-584.

Landys-Ciannelli, M.M., M. Ramenofsky, T. Piersma, J. Jukema, Castricum Ringing Group, and J.C. Wingfield. 2002. Baseline and stress-induced plasma corticosterone during long-distance migration in the bar-tailed godwit, *Limosa lapponica*. Physiological and Biochemical Zoology 75:101–110.

Lindstrom, A., M, Klaassen, T. Piersma, N. Holmgren, and L. Wennerberg. 2002. Fuel stores of juvenile waders on autimn migration in high arctic Canada. Ardea 90:93-101.

Lohmus, M.L., R. Sandberg, R.L. Holberton, and F.R. Moore. 2003. Corticosterone levels in relation to migratory readiness in red-eyed vireos (*Vireo olivaceus*). Behavioral Ecology and Sociobiology 54:233-239.

Marra, P.P., and R.L. Holberton. 1998. Corticosterone levels as indicators of habitat quality: effects of habitat segregation in a migratory birds during the non-breeding season. Oecologia 116:282-292.

Mori, J.G., and J.C. George. 1978. Seasonal changes in serum levels of certain metabolites, uric acid and calcium in the migratory Canada Goose *(Branta canadensis*). Comparative Biochemistry and Physiology 59:263-269.

Nebel, S., D.B. Lank, P.D. O'Hara, G. Fernandez, B. Haase, F. Delgado, F.A. Estela, L.J.E. Ogden, B. Harrington, B.E. Kus J.E. Lyons, F. Mercier, B. Ortego, J.Y. Takekawa, N. Warnock, and S.E. Warnock. 2002. Western sandpipers (*Calidris mauri*) during the nonbreeding season: spatial segregation on a hemispheric scale. Auk 119:922-928.

O'Hara, P.D., G. Fernandez, F. Becerril, H. de la Cueva, and D.B. Lank. 2005. Life history varies with migration distance in Western Sandpipers (*Calidris mauri*). Journal of Avian Biology 36:191-202.

O'Hara, P.D., D.B. Lank, and F.S. Delgado. 2002. Is the timing of moult altered by migration? Evidence from a comparison of age and residency classes of Western Sandpipers (*Calidris mauri*) in Panama. Ardea 90:61-70.

O'Hara, R.B., and D.J. Kotze. 2010. Do not log-transform count data. Methods in Ecology and Evolution 1: 118-122.

O'Reilly, K.M., and J.C. Wingfield. 2003. Seasonal, age, and sex differences in weight, fat reserves, and plasma corticosterone in Western Sandpipers. Condor 105:13-26.

Payne, R.B. 1972. Mechanisms and control of moult. In: D.S. Farner and J.R. King, eds. Avian Biology, Vol. 5. New York: Academic Press.

Piersma, T., J. Reneerkens, and M. Ramenofsky. 2000. Baseline corticosterone peaks in shorebirds with maximal energy stores for migration: a general preparatory mechanism for rapid behavioral and metabolic transitions? General and Comparative Endocrinology 120: 118–126.

Prater, A.J., J.H. Marchant, and J. Vuornen. 1977. Guide to the identification and aging of holarctic waders. Field Guide No. 17, British Trust for Ornithology, Tring, U.K.

R Foundation for Statistical Computing. 2010. R version 2.12.1.

Ramenofsky, M. 1990. Fat storage and fat metabolism in relation to migration. In: E. Gwinner, Ed. Bird Migration: the Physiology and Ecophysiology:331-351. Berlin: Springer-Verlag.

Romero, L.M. 2002. Seasonal changes in plasma glucocorticoid concentrations in free-living vertebrates. General and Comparative Endocrinology 128:1-24.

Romero, L.M., and J.M. Reed. 2004. Collecting baseline corticosterone samples in the field: is under 3 min good enough? Comparative Biochemistry and Physiology A: Molecular and Integrative Physiology 140:73–79.

Romero, L.M., D. Strochlic, and J.C. Wingfield. 2005. Corticosterone inhibits feather growth: potential mechanism explaining seasonal down regulation of corticosterone during molt. Comparative Biochemistry and Physiology, Part A 142:65-73.

Schaub, M., and L. Jenni. 2001. Variation of fuelling rates among sites, days, and individuals in migrating passerine birds. Functional Ecology 15:584-594.

Schneider, D.C., and B.A. Harrington. 1981. Timing of shorebird migration in relation to prey depletion. Auk 98:801-811.

Schwabl, H., F. Barlein, and E. Gwinner. 1991. Basal and stress-induced corticosterone levels of Garden Warblers, *Sylvia borin*, during migration. Journal of Comparative Physiology B 161:576-580.

Stevens, L. 1996. Avian biochemistry and molecular biology. Cambridge: Cambridge University Press.

Stillman, R.A., A.D. West, J.D. Goss-Custard, S. McGrorty, N.J. Frost, D.J. Morrisey, A.J. Kenny, and A.L. Drewitt. 2005. Predicting site quality for shorebird communities: a case study on the Humber estuary, UK. Marine Ecology Progress Series 305:203-217.

Taylor, A.R., R.B. Lanctot, A.N. Powell, F. Huettmann, D.A. Nigro, and S.J. Kendall. 2010. Distribution and community characteristics of staging shorebirds on the northern coast of Alaska. Arctic 63:451-467.

Taylor, C.M., D.B. Lank, A.C. Pomeroy, and R.C. Ydenberg. 2007. Relationship between stopover site choice of migrating sandpipers, their population status, and environmental stressors. Israel Journal of Ecology and Evolution 53:245-261.

Totzke, U. and F. Bairlein. 1998. The body mass cycle of the migratory garden warbler (*Sylvia borin*) is associated with changes in basal plasma metabolite levels. Comparative Biochemistry and Physiology (A) 121:127 -133.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893-901.

Warnock, N. 2010. Stopping vs. staging: the difference between a hop and a jump. Journal of Avian Biology 41:621-626.

Warnock, N.D., and R.E. Gill. 1996. Dunlin (*Calidris alpina*). In: A. Poole, ed. The Birds of North America Online. Ithaca: Cornell Lab of Ornithology. Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/203; DOI:10.2173/bna.203.

Williams, T.D., C.G. Guglielmo, O. Egeler, and C. J. Martyniuk. 1999. Plasma lipid metabolites provide information on mass change over several days in captive western sandpipers. Auk 116:994-1000.

Williams, T.D., N Warnock, J.Y. Takekawa, and M.A. Bishop. 2007. Flyway-scale variation in plasma triglyceride levels as an index of refueling rate in spring-migrating Western Sandpipers (*Calidris mauri*). Auk 124:886-897.

Wilson, W. H. 1994. Western Sandpiper (*Calidris mauri*). In: A. Poole, ed. The Birds of North America Online. Ithaca: Cornell Lab of Ornithology. Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/090; DOI:10.2173/bna.90.

Wingfield, J.C., C.M. Vleck, and M.C. Moore. 1992. Seasonal changes in the adrenocortical responses to stress in birds of the Sonoran Desert. Journal of Experimental Zoology 264:419-428.

Winker, K., D.W. Warner, and A.R Weisbrod. 1992. Daily mass gains among woodland migrants at an inland stopover site. Auk 109:853-862.

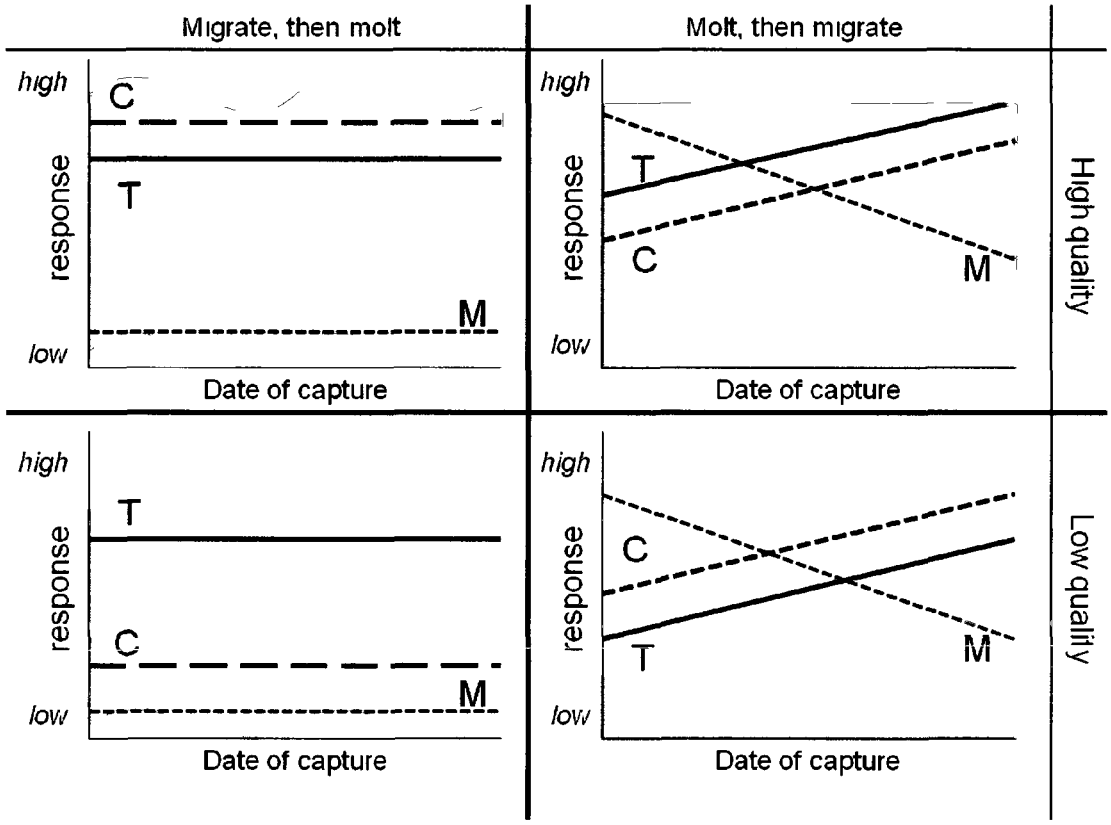


Figure 4.1. Predictions for molt intensity (M, dotted lines), triglyceride levels (T, solid lines), corticosterone levels (C, dashed lines), and density (D, shaded regions). Predictions are made by Julian date of capture. Panels are organized according to molt strategy (top) and site quality (right side). Y-axis values range from low to high but hypothetical units vary with metric.

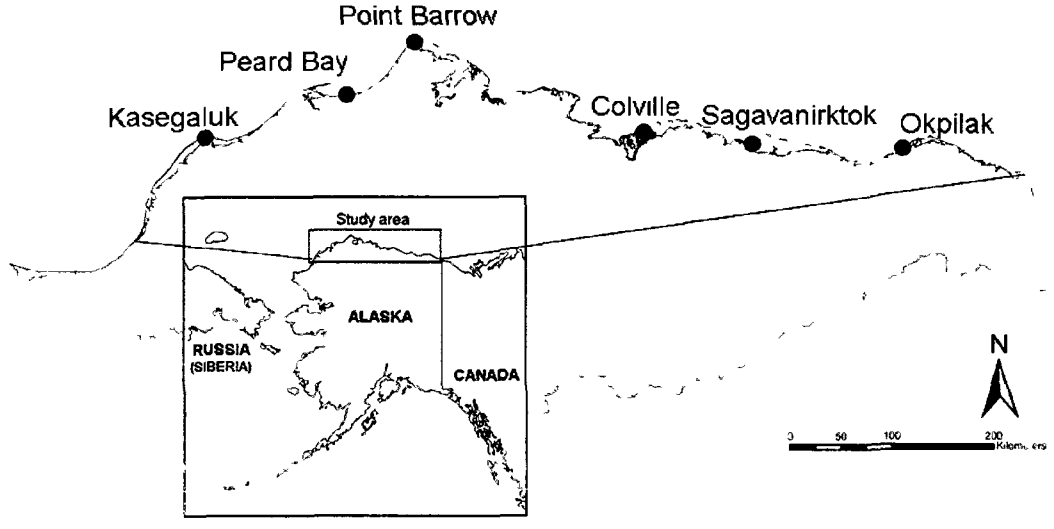


Figure 4.2. Map of northern Alaska study area showing locations of field sites.

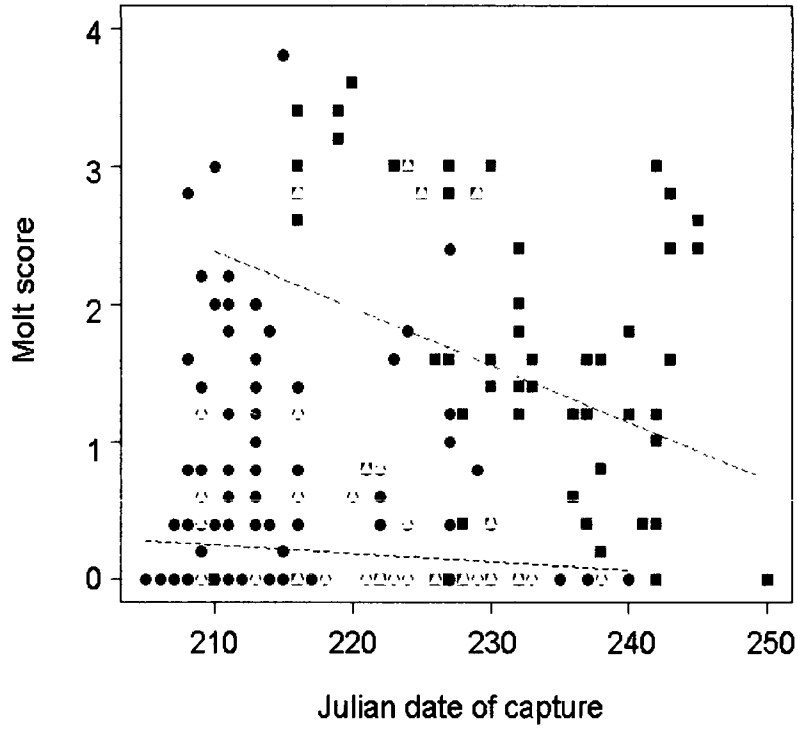


Figure 4.3. Scatterplot of molt intensity vs. date of capture for each species. Dunlin = squares and top line; Semipalmated Sandpiper = circles and bottom line; Western Sandpiper = triangles and middle line.

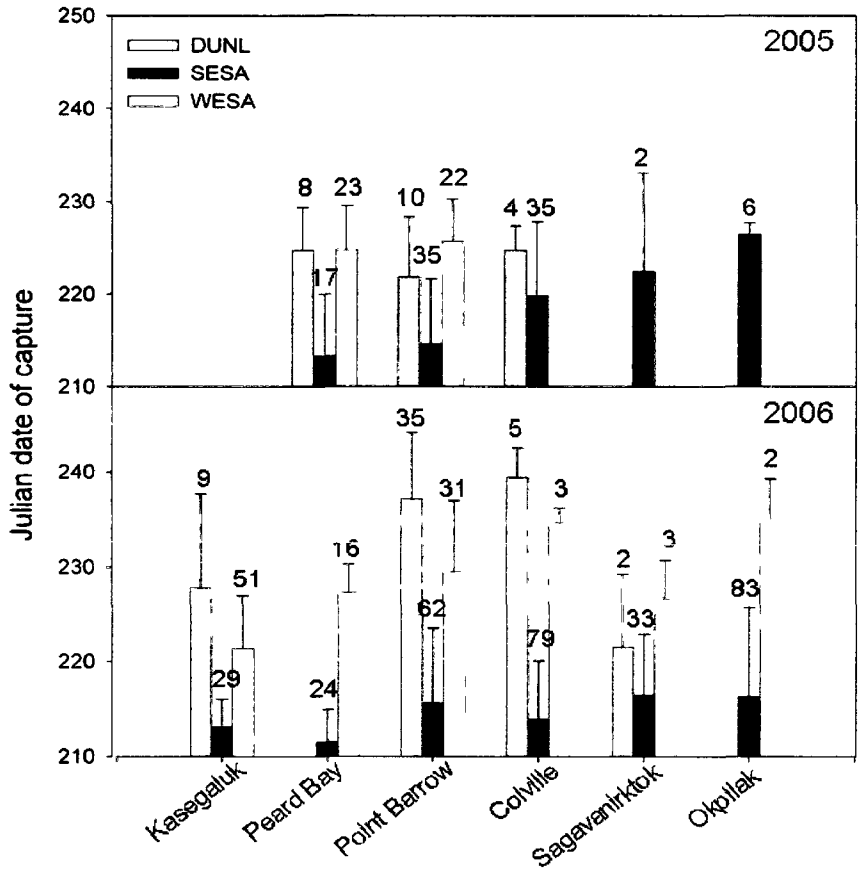
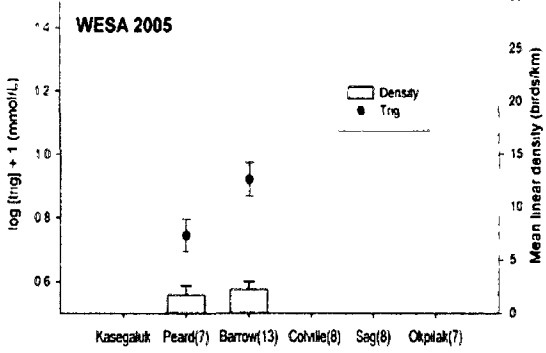
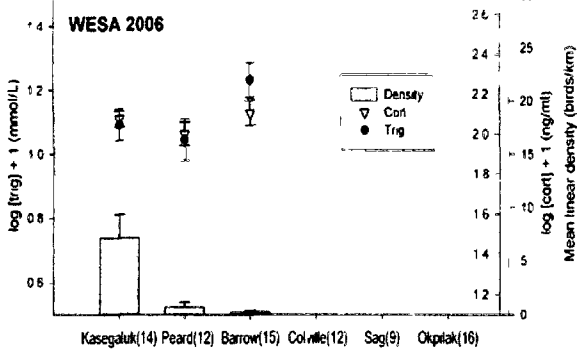


Figure 4.4. Mean date of capture by year, site, and species. Error bars indicate one standard error of the mean. Sample sizes are given above each corresponding bar. DUNL = Dunlin; SESA = Semipalmated Sandpiper; WESA = Western Sandpiper.


WESA 2005
log [trig] + 1 (mmol/L)
Mean linear density (birds/km)
Density
Trig
Kasegaluk
Peard(7)
Barrow(13)
Colville(8)
Sag(8)
Okpilak(7)


WESA 2006
log [trig] + 1 (mmol/L)
log [cort] + 1 (ng/ml)
Mean linear density (birds/km)
Density
Cort
Trig
Kasegaluk(14)
Peard(12)
Barrow(15)
Colville(12)
Sag(9)
Okpilak(16)

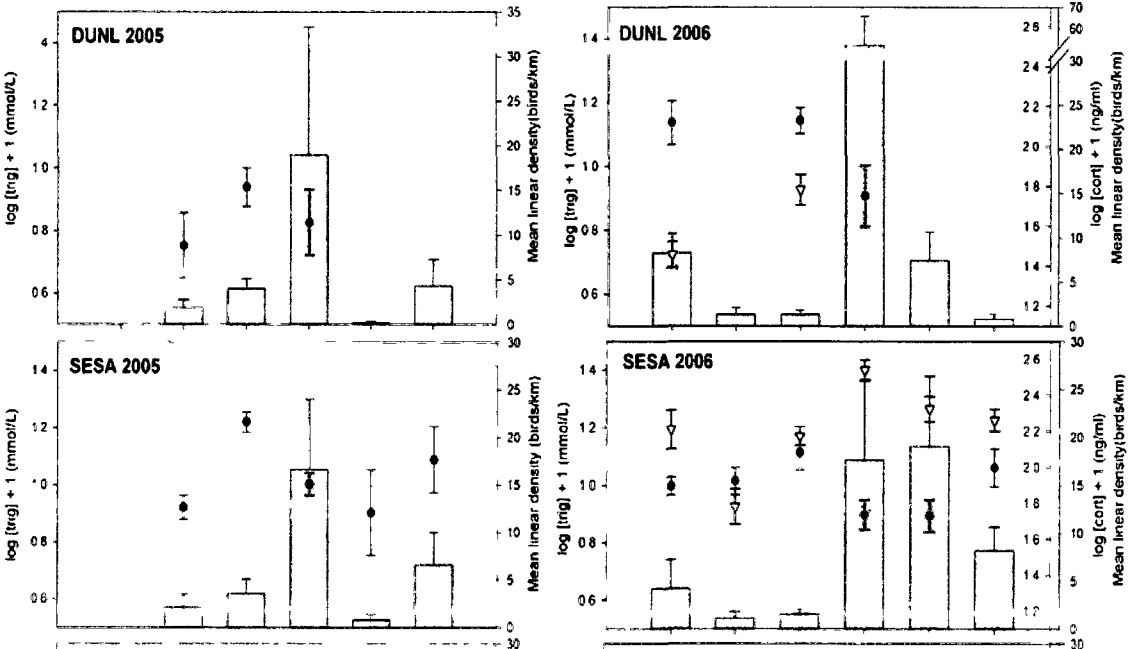
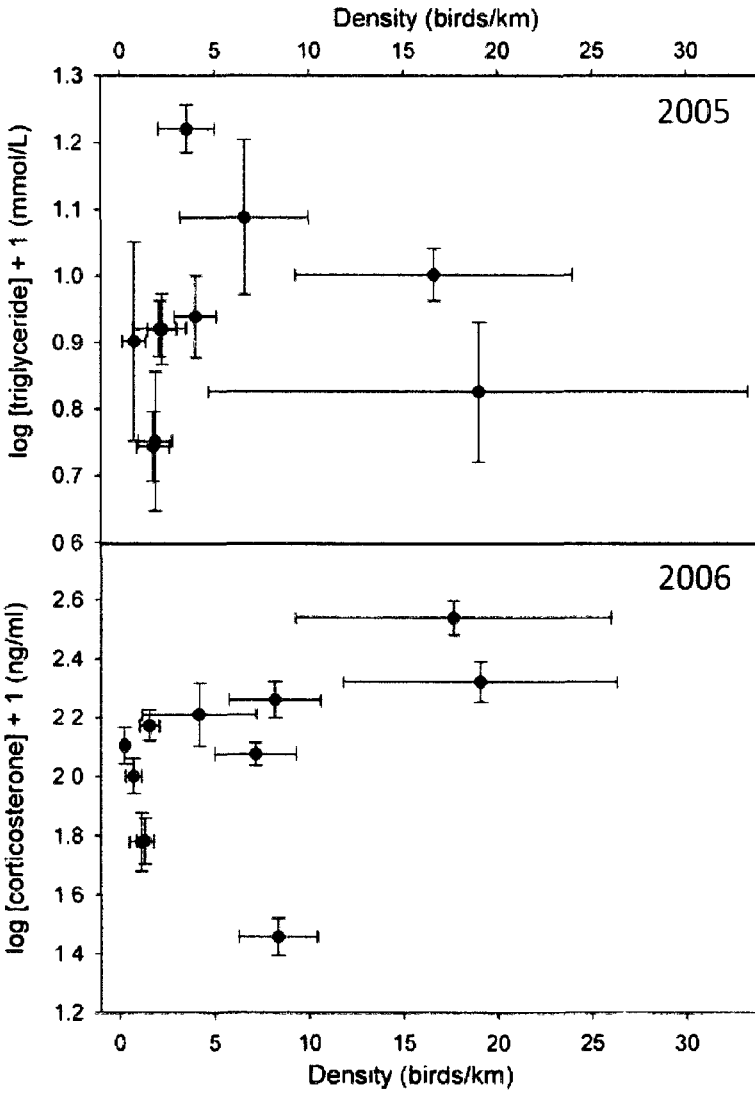

DUNL 2005
DUNL 2006
SESA 2005
SESA 2006
log [trig] + 1 (mmol/L)
log [cort] + 1 (ng/ml)
Mean linear density(birds/km)
Mean linear density (birds/km)

Figure 4.5. Triglyceride and corticosterone levels, and mean linear densities (averaged across each season) for three species of shorebirds on the northern coast of Alaska in 2005-2006. Error bars show one standard error of the mean for all variables. DUNL = Dunlin, SESA = Semipalmated Sandpiper, and WESA = Western Sandpiper. Sag = Sagavanirktok. Number of surveys used to calculate linear density for each species at each site are given in parentheses after site names at bottom of graph. Sample sizes for density surveys at each site are given along x-axis. Sample sizes for physiology metrics are given in Table 4.1.


Density (birds/km)
0
5
10
15
20
25
30
2005
log [triglyceride] + 1 (mmol/L)
1.3
1.2
1.1
1.0
0.9
0.8
0.7
0.6
2006
log [corticosterone] + 1 (ng/ml)
2.6
2.4
2.2
2.0
1.8
1.6
1.4
1.2
Density (birds/km)

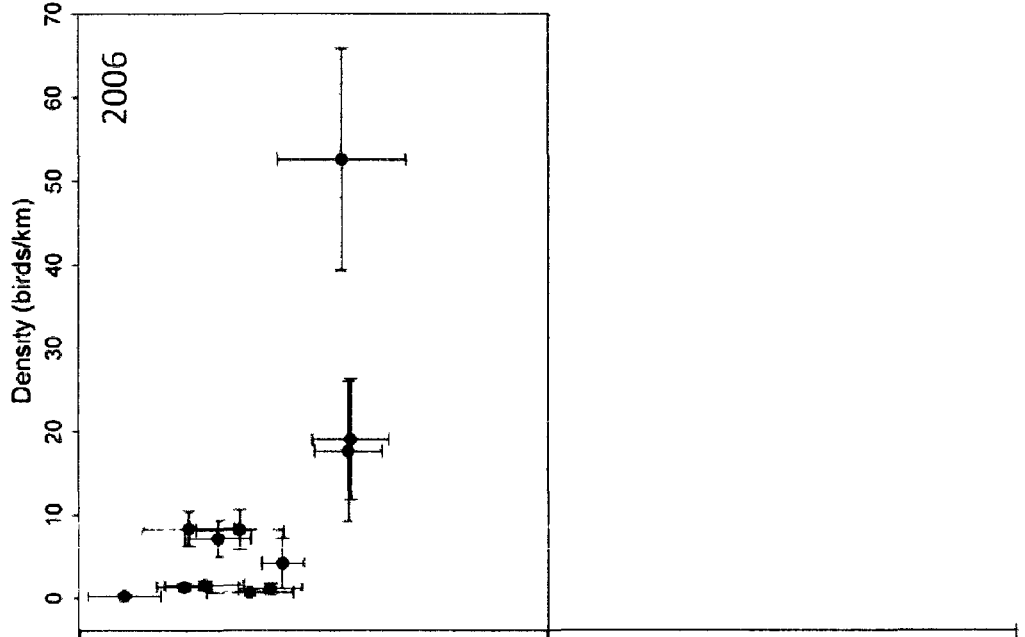

2006
Density (birds/km)
0
10
20
30
40
50
60
70

Figure 4.6. Relationships between mean site-specific linear density and triglyceride levels in 2005 (top left), linear density and triglyceride levels in 2006 (top right), and linear density and corticosterone levels in 2006 (bottom). Each data point represents paired means for a given site for the two variables represented on the axes of the graph. Dunlin = black symbols, Semipalmated Sandpipers = red symbols, Western Sandpipers = blue symbols. Error bars indicate one standard error of the mean for all variables. Sample sizes are given in Table 4.1.

Table 4.1. Sample sizes for shorebirds captured on north coast of Alaska, 2005-2006, overall and for physiological analysis. "Captured" refers to the total number of individuals captured at each site; "Trig" refers to the number of individuals sampled for triglyceride levels; "Cort" refers to the number of individuals sampled for baseline corticosterone levels.

	Kasegaluk		Peard Bay		Pt Barrow		Colville		Sag		Okpilak	
Species	2005	2006	2005	2006	2005	2006	2005	2006	2005	2006	2005	2006
Dunlin												
Captured	NA	9	8	0	10	35	4	5	0	2	0	0
Trig	NA	8	8	0	10	31	4	2	0	0	0	0
Cort	NA	6	NA	0	NA	31	NA	1	NA	1	NA	0
Semipalmated Sandpiper												
Captured	NA	29	17	24	35	62	35	79	2	33	6	83
Trig	NA	19	17	19	35	22	35	23	2	19	6	20
Cort	NA	8	NA	8	NA	35	NA	16	NA	4	NA	19
Western Sandpiper												
Captured	NA	51	23	16	22	31	0	3	0	3	0	2
Trig	NA	17	23	12	22	17	0	0	0	0	0	0
Cort	NA	12	NA	5	NA	25	NA	0	NA	0	NA	0

Table 4.2. Model selection results for triglyceride levels by species. Models within 10% of the Akaike weight of the top model are shown. All models included mass, tarsus length, and bleed time in addition to the parameters listed. Columns at right show model selection criteria including K (number of parameters), Akaike's Information Criterion corrected for small sample sizes (AIC_c), ΔAIC_c (difference in AIC_c units between given model and model with lowest AIC_c), relative likelihoods (rel L), Akaike weights (w_i), and adjusted R-squared. Models are ranked by Akaike weights, although model-averaging procedures were used for parameter estimation due to >1 model having substantial w_i. The best + molt model shows the ΔAIC_c between the top model alone and with the molt intensity variable added. A positive ΔAIC_c value for this comparison indicates the model with molt added does not show improved fit; a negative ΔAIC_c value shows the opposite.

Species	Model	K	AICc	ΔAICc	rel *L*	ω_i	adj R^2
DUNL	Date, year, date*year	7	-13.732	0.000	1.000	0.221	0.320
	Site	5	-13.366	0.366	0.833	0.184	0.301
	Site, date	6	-12.563	1.169	0.557	0.123	0.308
	Site, year	6	-12.561	1.171	0.557	0.123	0.308
	Year	5	-12.404	1.328	0.515	0.114	0.265
	Site, date, site*date	7	-12.137	1.595	0.451	0.100	0.341
	Site, year, site*year	7	-10.641	3.091	0.213	0.047	0.303
	Site, date, year	7	-10.409	3.322	0.190	0.042	0.300
	Date, year	6	-9.898	3.834	0.147	0.033	0.250
	Best + molt	**8**	**-16.765**	**-3.033**			**0.375**
SESA	Site, date	6	-58.663	0.000	1.000	0.492	0.269
	Site	5	-56.800	1.863	0.394	0.194	0.259
	Site, date, year	7	-56.522	2.141	0.343	0.169	0.266
	Site, year	6	-54.895	3.768	0.152	0.075	0.256
	Best + molt	**7**	**-55.060**	**3.603**			**0.274**
WESA	Site, year	6	-25.183	0.000	1.000	0.550	0.449
	Site, date, year	7	-23.542	1.640	0.440	0.242	0.446
	Site, year, site*year	7	-22.900	2.282	0.319	0.176	0.442
	Best + molt	**7**	**-26.764**	**-1.582**			**0.466**

Table 4.3. Model selection results for corticosterone levels by species. Models within 10% of the Akaike weight of the top model are shown. All models included body mass and tarsus in addition to parameters listed; a model given by (.) indicates that only body mass and tarsus were included. Columns at left show variables included in model set; columns at right show model selection criteria. Models are ranked by Akaike weights (w_i), although model-averaging procedures were used for parameter estimation due to >1 model having substantial w_i. The best + molt model shows the ΔAIC_c between the top model alone and with the molt intensity variable added. A positive ΔAIC_c value for this comparison indicates the model with molt added does not show improved fit; a negative ΔAIC_c value shows the opposite.

Species	Model	K	AIC_c	ΔAIC_c	rel L	w_i	adj R^2
DUNL	Site	4	29.281	0.000	1.000	0.418	0.091
	(.)	3	29.696	0.415	0.813	0.339	0.036
	Site, date	5	31.710	2.429	0.297	0.124	0.071
	Date	4	32.313	3.032	0.220	0.092	0.004
	Best + molt	**5**	**31.763**	**2.481**			**0.070**
SESA	Site, date	5	-9.958	0.000	1.000	0.589	0.510
	Site	4	-9.180	0.778	0.678	0.399	0.499
	Best + molt	**6**	**-7.664**	**2.294**			**0.504**
WESA	(.)	3	0.490	0.000	1.000	0.412	-0.023
	Date	4	0.504	0.014	0.993	0.409	0.012
	Site, date	5	3.119	2.629	0.269	0.111	0.008
	Site	4	4.433	3.943	0.139	0.057	-0.065
	Best + molt	**5**	**0.085**	**1.261**			**-0.006**

5. Conclusions

> Thus, food availability, foraging activity, staging time, and fattening rates by Arctic migrants are all interrelated in the adaptation for migrating great distances to the Arctic…
>
> -Johnson and Herter, 1990

> Biodiversity is the wellspring for comparisons, and insightful comparison is the basis for much of our understanding in biology.
>
> -E.O. Wilson, *The Diversity of Life,* 1992

In this dissertation I have attempted to elucidate the geographic and ecological use of the ACP of Alaska by postbreeding shorebirds. The three data chapters (Chapters 2-4) collected herein reported on numerous characteristics of both individual birds (e.g., movement patterns, residence time, physiology) and of the community of shorebirds as a whole (e.g., distribution, diversity, phenology, and habitat use). Specifically, in Chapter 2, I identified persistent within- and between-year concentrations of postbreeding shorebirds at Peard Bay, Pt. Barrow/Elson Lagoon, Cape Simpson, and Smith Bay to Cape Halkett, and on the Sagavanirktok and Kongakut river deltas. I found that the

shorebird community was more even and diverse (evenness E and Shannon Weiner *H'*) along the Beaufort Sea compared to the Chukchi Sea and in 2005 versus 2006. Postbreeding shorebirds' phenology varied by species and location, and differed than that reported in previous studies for several species. My results also suggest the existence of three foraging habitat guilds among the shorebird species observed in this study: gravel beach, mudflat, and salt marsh/pond edge; these foraging associations appear to be conserved through time when compared to data collected in the mid-1970's.

In Chapter 3, I examined postbreeding movements of radio-equipped individuals and found that Semipalmated Sandpipers moved eastward, consistent with their ultimate migration direction, but movement patterns of other species were not entirely consistent with their ultimate migration directions. Timing of postnuptial molt appeared to have more influence over residence time and movements than did migration strategy (i.e., length of individual flight bouts). Post-capture residence time for Semipalmated Sandpipers was less than for Western Sandpipers and significantly less than for Dunlin, and movements between sites occurred more quickly and frequently for Semipalmated Sandpipers than Dunlin.

Lastly, in Chapter 4, I compared molt intensity and capture dates across three species of calidrid sandpipers and confirmed that Dunlin exhibited a "molt-then-migrate" strategy while Semipalmated Sandpipers exhibited a "migrate-then-molt" strategy. Western Sandpipers were found to be intermediate between these two species in molt strategy. Postbreeding sites in northern Alaska may function as stopover/resting sites for

Semipalmated Sandpipers and some Western Sandpipers, whereas they may function as staging/molting sites for Dunlin and other Western Sandpipers. Molt intensity had a larger influence on triglyceride levels for Dunlin compared to the other species. Sites differed in quality as assessed by both metrics, although the ranking of sites as high or low quality was not consistent across all species and metrics. Corticosterone was positively correlated with mean linear density at each site for Semipalmated Sandpipers only; triglyceride was not significantly correlated with density for any species. These results suggest that physiologic metrics should perhaps be used to confirm other assessments of site quality or in a long-term monitoring framework rather than as independent indicators of site or habitat quality.

As an example of using physiology in a confirmatory manner, and to provide a link between distribution patterns assessed in the second chapter and physiologically-based patterns of site quality from the fourth chapter, I examined whether birds captured at specific sites contained within noted concentration areas had levels of physiologic metrics that indicated higher site quality. Triglyceride levels were high at Barrow for Semipalmated Sandpipers (indicating high fueling rates), and the surrounding Pt. Barrow/Elson Lagoon sub-region had the highest per-interval counts of postbreeding shorebirds of any area of the ACP. However, triglyceride levels for Dunlin and corticosterone levels for Semipalmated Sandpipers were lower (indicating lower fueling rates and possibly lower migratory "readiness") at Peard Bay, despite the fact that this area was also designated as a postbreeding concentration area. And, corticosterone levels

for Semipalmated Sandpipers were high (potentially indicating high migratory "readiness") at the Colville Delta, but this area did not qualify as a postbreeding concentration area during my aerial surveys. Obviously, many factors play into how birds distribute themselves across a large region like the ACP, and physiologically-based site function or quality may be just one of these. Additionally, the scales at which data were collected for these two efforts (distribution patterns and physiologically-based site quality assessment) were very different, and the individual birds involved in each assessment (all individuals for distribution, only three calidrid species for physiology) varied, so direct comparisons between these data may not be completely appropriate.

A common theme throughout this research was variability on a species-specific basis. Through use of a comparative, community-scale approach to investigating postbreeding ecology, I have shown that shorebird species differ widely in their use of the ACP prior to fall migration. For a suite of similar calidrid sandpipers (Dunlin [*Calidris alpina*], Semipalmated Sandpipers [*C. pusilla*], and Western Sandpipers [*C. mauri*]), and likely for other species I did not study in as much depth, this variation is mediated by differences in each species' life history strategies governing the timing of important life history events.

These differences in the life history strategies, and therefore patterns of behavior and ecology, of Arctic-breeding shorebird species all using the same landscape have likely evolved due to a number of selective pressures. Foremost, the overall length and nature of each species' migration between temperate and tropical wintering areas and

Arctic breeding grounds places constraints on the scheduling of life history events due to the need to prepare for long-distance flights by acquiring adequate fuel reserves (Piersma 2007), and to ensure that feathers are in good enough condition for long distance flight (Thompson and Leu 1994). Weather conditions deteriorate in late summer in the Arctic, and coastal zones become subject to fall storms that result in frequently changing water levels which inundate (and make unpredictable) potential foraging sites (Holmes 1966, Connors 1984), and could slow fueling rates for shorebirds. Ecological constraints on food availability at tropical coastal wetlands (as evidenced by low fueling rates, van Gils et al. 2005) may affect shorebirds' ability to produce high quality feathers, thus early arrival at wintering areas may confer an advantage if it reduces intra- or interspecific competition during molt (O'Hara et al. 2002). Holmes (1966) hypothesized that Dunlin, by remaining longer in the Arctic after breeding than other species, were able to take advantage of an abundant food supply to molt and replenish resources at a time when few competitors were present, and that this longer stay was made possible by their relatively short migration distance. On the other hand, Semipalmated Sandpipers, which undertake long overall migrations to tropical wintering areas, may be under selection to prepare for migration quickly and leave the Arctic relatively early (before conditions deteriorate and competition builds at wintering areas) to migrate south. I found that Western Sandpipers exhibit a set of strategies and behaviors intermediate to those of Dunlin and Semipalmated Sandpipers, likely because their migration distance is intermediate between these two species.

While *articola* Dunlin breeding on the ACP of Alaska have longer migrations than the *pacifica* Dunlin of which Holmes was thinking, my research also demonstrated that at least some *arcticola* Dunlin fly a relatively short distance to the Yukon Kuskokwim Delta on their first leg of migration, where they are thought to stage prior to migrating to Asia (Warnock and Gill 1996). Thus the length of the first migratory flight out of the Arctic to staging or stopover sites with more abundant or predictable resources or less variable weather conditions may also have an important influence on molt and migration schedules, in addition to the overall length of each species' migration.

These patterns suggest that the postbreeding period for Arctic-breeding shorebirds on the ACP of Alaska is influenced not only by the timing of breeding and chick rearing (Holmes 1971, Holmes 1972), but also by factors affecting migration timing and distance. I was able to study these patterns for only a subset of the common shorebirds of the ACP. However, it would be a fruitful area of research to see whether other Arctic-breeding species for which we have less natural history information also conform to patterns of behavior and physiology that may be predicted from their migration distances and life history strategies.

Differences in postbreeding ecology and behavior may be advantageous in that they enable shorebird species to minimize their overlap in use of, and therefore competition for, limited coastal foraging resources in northern Alaska. Huge numbers of shorebirds breed on the Arctic tundra each summer (Callaghan et al. 2004, Alaska Shorebird Group 2008), probably because this vast region provides abundant nesting

habitat that may be limited only by predation rather than by nest sites or territories (e.g., Smith et al. 2007), and because disease organisms and vectors (particularly parasites) may be less common in the Arctic than in temperate regions (Ridley 1993, Piersma 1997). However, coastal areas in northern Alaska are more limited in extent than the tundra, and the quality and/or predictability of these areas may be more variable. Thus, littoral habitat that enables individuals to adequately prepare for migration may be limiting for pre-migratory shorebirds, and it could be advantageous for each species' fitness that their behavior and requirements in the Arctic after the breeding season are varied.

This theme of species-specific variability in postbreeding ecology has implications for both future research activity in the Arctic and for management and conservation of migratory shorebird populations. Estimates of population size for postbreeding shorebirds or densities at particular sites or habitats have often been reported for all birds or for simple size categories (e.g. "small shorebirds"), particularly during aerial surveys of larger geographic areas (Spindler 1979, Johnson et al. 1993, Taylor et al. 2010). This has led to postbreeding shorebirds being usually considered as a single category of avifauna in assessments of the affected environment during National Environmental Protection Act consultations for oil and gas exploration of the ACP. With knowledge of individual species' behavior during the postbreeding period, population estimates and impact assessments may be conducted for species or suites of similar species, for which effects of habitat loss or degradation may not be the same. Future

research could examine how habitat use, population size, or other characteristics of shorebird ecology on the ACP changes through the postbreeding period, which was something I was unable to address in this study.

How migratory shorebirds use distinct sites or habitats during their migrations to and from Arctic breeding areas in part determines what sites are targeted for management or conservation action. Sites that are used for a long period of time or by a large proportion of a species or population (i.e., staging areas where individual birds replenish fuel stores prior to or during migration) have been considered to be "ecological bottlenecks" (Myers 1983), and many of these have been recognized by international conservation efforts such as the Western Hemisphere Shorebird Reserve Network (www.whsrn.org) or Important Bird Area program (www.birdlife.org/action/science/) (Harrington and Perry 1995, Plissner et al. 2000). Therefore, a number of authors have attempted to define what constitutes staging vs. stopover sites for migratory birds (Skagen and Knopf 1994, Warnock and Bishop 1998, Warnock 2010). Typically these arguments have centered around characteristics of the site or the birds using the site. For example, Warnock (2010) described staging sites as being characterized by large size, high and predictable prey quantity/quality, high fueling rates, and long length of stay by individual birds, whereas stopover sites have the opposite (or different) characteristics. However, these site-specific definitions must not be taken to imply that all migratory birds use a given site in a similar way. Through this research I showed that the same sites may be used by different species for varying purposes and lengths of time, such that some

species may stage at numerous interconnected sites within a region (e.g. Dunlin) whereas other species may not stage in a given location or region at all (e.g. Semipalmated Sandpipers). It is critical to effective management and conservation of shorebirds as a taxa that we consider how individual species tend to use sites throughout their annual cycles, and that habitat protection programs acknowledge the importance of dispersed and shifting distributions of shorebirds across a landscape as well as congregations of birds at major staging areas (Skagen et al. 2005).

Finally, I wish to note that the data collected throughout this study have been made available to interested resource management agencies in Alaska, and the associated metadata for the aerial surveys (written to FDGC standards) will be hosted online to facilitate further access. To date, these data have been used to inform environmental assessments for the National Petroleum Reserve-Alaska, for inclusion in a nomination package to the Western Hemisphere Shorebird Reserve Network for the barrier islands and lagoons of the northeast Alaska coast, and to describe the importance of the Arctic Plains and Mountains Bird Conservation Region to shorebirds for the updated Alaska Shorebird Conservation Plan (Alaska Shorebird Group 2008). It is a pleasure to see results from this project being used in the conservation and management arena as my ultimate reason for becoming a scientist has always been to make a difference to the organisms I study.

Literature cited

Alaska Shorebird Group. 2008. Alaska Shorebird Conservation Plan. Version II. Anchorage, AK: Alaska Shorebird Group.

Callaghan, T.V., L.O. Bjorn, Y. Chernov, T. Chapin, T.R. Christensen, et al. 2004. Biodiversity, distributions, and adaptations of Arctic species in the context of environmental change. Ambio 33:404-417.

Connors, P.G. 1984. Ecology of shorebirds in the Alaskan Beaufort littoral zone. In: P.W. Barnes, D.M. Schell and E. Reimnitz, eds. The Alaskan Beaufort Sea: Ecosystems and Environments. New York: Academic Press.

Harrington, B., and E. Perry. 1995. Important shorebird staging sites meeting WHSRN criteria in the U.S. Manomet Center for Conservation Sciences and U.S Fish and Wildlife Service, unpublished report.

Holmes, R.T. 1966. Breeding ecology and annual cycle adaptations of the Red-backed Sandpiper (*Calidris alpina*) in northern Alaska. Condor 68:3-46.

Holmes, R.T. 1971. Latitudinal differences in the breeding and molt schedules of Alaskan Red-backed Sandpipers (*Calidris alpina*). Condor 73:93-99.

Holmes, R.T. 1972. Ecological factors influencing the breeding season schedule of Western Sandpipers (*Calidris mauri*) in subarctic Alaska. American Midland Naturalist 87:472-491.

Johnson, S.R., and D.R. Herter. 1990. Bird migration in the Arctic: a review. In: E. Gwinner, ed. Bird Migration: Physiology and Ecophysiology. Berlin: Springer-Verlag.

Johnson, S.R., D.A. Wiggins, and P.F. Wainwright. 1993. Late-summer abundance and distribution of marine birds in Kasegaluk Lagoon, Chukchi Sea, Alaska. Arctic 46:212-227.

Myers, J.P. 1983. Conservation of migrating shorebirds: staging areas, geographic bottlenecks, and regional movements. American Birds 37:23-25.

O'Hara, P.D., D.B. Lank, and F.S. Delgado. 2002. Is the timing of moult altered by migration? Evidence from a comparison of age and residency classes of Western Sandpipers *Calidris* mauri in Panama. Ardea 90:61-70.

Piersma, T. 1997. Do global patterns of habitat use and migration strategies co-evolve with relative investments in immunocompetence due to spatial variation in parasite pressure? Oikos 80:623-631.

Piersma, T. 2007. Using the power of comparison to explain habitat use and migration strategies of shorebirds worldwide. Journal of Ornithology 148 (Supplement 1):S45-S59.

Plissner, J.H., S.M. Haig, and L.W. Oring. 2000. Postbreeding movements of American Avocets and implications for wetland connectivity in the western Great Basin. Auk 117:290-298.

Ridley, M. 1993. The red queen: sex and the evolution of human nature. London: Viking Press.

Skagen, S.K., and F.L. Knopf. 1994. Residency patterns of migrating sandpipers at a midcontinental stopover. Condor 96:949-958.

Skagen, S.K., S. Brown, and R. Johnson. 2005. Implications of different shorebird migration strategies for habitat conservation. USDA Forest Service General Technical Report PSW-GTR-191.

Smith, P.A., H.G. Gilchrist, and J.N.M. Smith. 2007. Effects of nest habitat, food, and parental behavior on shorebird nest success. Condor 109-15-31.

Spindler, M.A. 1979. Bird populations in coastal habitats, Arctic National Wildlife Range, Alaska: results of 1978 and 1979 aerial surveys. Unpublished report, available from the U.W. Fish and Wildlife Service, Arctic National Wildlife Refuge, 101 12th Ave., Fairbanks, AK 99701.

Taylor, A.R., R.B. Lanctot, A.N. Powell, D.A. Nigro, and S.J. Kendall. 2010. Distribution and community characteristics of staging shorebirds on the northern coast of Alaska. Arctic 63:451-467.

Thompson, C.W., and M. Leu. 1994. Determining homology of molts and plumages to address evolutionary questions: a rejoinder regarding emberizid finches. Condor 96:769-782.

van Gils, J.A., P.F. Battley, T. Piersma, and R. Drent. 2005. Reinterpretation of gizzard sizes of Red Knots world-wide emphasizes overriding importance of prey quality at migratory stopover sites. Proceedings of the Royal Society B 272:2609-2618.

Warnock, N. 2010. Stopping vs. staging: the difference between a hop and a jump. Journal of Avian Biology 41:621-626.

Warnock, N., and M.A. Bishop. 1998. Spring stopover ecology of migrant Western Sandpipers. Condor 100:456-467.

Warnock, N.D., and R.E. Gill. 1996. Dunlin (*Calidris alpina*). *In* A. Poole and F. Gill, eds. The Birds of North America, No. 203. The Birds of North America, Inc., Philadelphia, PA.

Wilson, E.O. 1992. The diversity of life. Cambridge: Harvard University Press.